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Understanding the causes of variation in reproductive expenditure in female St. Kilda Soay sheep: a focus on the role of space use and genetic differences

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Declaration

The work described in this thesis has been carried out by myself with guidance from my supervisors, unless otherwise stated and detailed below. The thesis is of my own composition and has not been submitted for any other degree or professional qualification.

Chapter 2 - data collection was led by CE Regan with assistance from E Damasceno, K Dicks, W Fincham, X Bal, P Hopper, and R Steenson, and guidance from JG Pilkington. CE Regan carried out the statistical analysis and wrote the manuscript with guidance from PT Smiseth and JM Pemberton, and completed edits with their input.

Chapter 3 - data used in this chapter come from the long-term data collection which has involved contributions from many people over the past 32 years. CER performed all the statistical analysis and wrote the manuscript with guidance and revisions from PTS.

Chapter 4 - this chapter also uses the long-term Soay sheep data. CER conducted all statistical analysis with guidance from AJ Wilson, and assistance from J Hadfield and D Nussey. CER wrote the manuscript with input from AJW, PTS, and JMP, and carried out edits with their guidance.

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Lay summary

Within the natural world, species show profoundly different reproductive patterns. For example, female African elephants reach sexual maturity at around 10 years old, produce a single, large offspring approximately every four years, provisioning these offspring for 22 months before birth and for several years after birth. In contrast, sockeye salmon spend around two years maturing at sea before returning to freshwater to engage in a single reproductive attempt in which they produce thousands of eggs. Even individuals of the same species often vary substantially in aspects of their reproduction and understanding the causes of this variation is important for understanding how differences in individual reproductive success affect population growth and stability, and the evolution of traits in natural populations. Although there has been substantial research into some of the potential causes of variation in individual reproduction, others have received much less attention. For example, little is known about how differences between individuals, in terms of their genetics and/or the way in which they use space and therefore access resources, influence investment into reproduction in the wild, particularly in terms of the care provided by parents. In this thesis, I use the detailed data available for the feral population of Soay sheep on the island of Hirta (St. Kilda, Scotland) to understand how differences between individuals, due to their genetics and contrasting access to resources influence a female's investment before and after birth. I found that a female's home range quality (measured as the availability of a key grassland community) was not significantly associated with the behaviour of either her or her lamb over the maternal care period, lamb growth between birth and weaning, or maternal body condition at the end of the maternal care period. This suggests that females with different quality home ranges provide their lambs with similar levels of care. Although I found that Soay sheep females that expend more resources on reproduction are less likely to survive the winter, I also found that female's with poorer quality home ranges did not incur greater costs of

reproduction compared to females with high quality home ranges. They were just as likely to survive the winter, and to reproduce the following year; however, I did find that females with high quality home ranges were more likely to produce twins. I also show that individuals with more similar home ranges tend to be more physically similar, for example in their jaw lengths, and have lambs that are also more similar in their birth dates, birth weights, and August weight. Nevertheless, incorporating this source of similarity into models estimating the genetic component of trait variation does not produce different results. Finally, I found that maternal genetics were an important contributor to variation in lamb growth and that this may be caused by maternal care behaviour having a genetic basis. In conclusion, I have shown that differences between female Soay sheep, in terms of their genetics and space use, are associated with between-individual variation in reproduction, but that genetic differences are more strongly associated with parental care variation than differences in space use.

Abstract

Reproductive patterns in the natural world are highly variable both between- and within-species. For example, mammalian females within a single population often vary substantially in their expenditure into offspring, both before and after birth. Understanding the causes of variation in reproductive behaviour remains a key aim within evolutionary ecology, due to its implications for understanding many aspects of biology, from population dynamics to life-history evolution. Nonetheless, little is known about how genetic differences between individuals and variation in individual space use influence investment into reproduction in the wild, particularly in terms of the parental care provided by females during lactation. In this thesis, I use the detailed phenotypic, relatedness, and census data available for the feral population of Soay sheep on the island of Hirta (St. Kilda, Scotland) to understand how differences between individuals driven by variation in genetics and access to resources influence a female's investment before and after birth. First, I present a field behavioural study to understand how a female's home range quality influenced maternal and lamb behaviour over the maternal care period. Despite previous work indicating that females with greater access to high quality vegetation had higher lifetime reproductive success, I found no evidence to suggest that home range quality influenced a mother's investment into care. Second, I used existing data to understand whether an individual's access to high quality vegetation influenced the costs incurred as a result of reproduction. Although I found evidence for significant survival costs, and identified reproductive costs for old animals in poor years, home range quality had no effect on the costs experienced by females. Nevertheless, I did find evidence that females with high quality home ranges were more likely to bear twins and this may explain the positive relationship between home range quality and lifetime reproductive success. Third, I explored methods for accounting for space sharing by related females within quantitative genetic analyses of three early-life (birth weight, birth

date, and August weight) and two adult traits (jaw length and metacarpal length). This enabled me to understand the importance of spatial sources of phenotypic similarity in these traits, and to derive estimates of genetic variance components that were not biased by failing to incorporate the space sharing of related females. Females that used space more similarly tended to be more phenotypically similar and had lambs that had more similar trait values. However, contrary to my expectation accounting for home range overlap had little influence on heritability estimates. Finally, I used the models described above to select females that varied in their genetic merit for lamb growth. These females were then included in a second field study to understand whether genetically mediated differences in lamb growth were caused by variation in maternal care behaviours that were, to some degree, genetically determined. Females whose genetic merit was associated with faster lamb growth were less likely to reject sucking attempts and had lambs that spent more time resting, suggesting that maternal care in this population may have a genetic basis. I finish by discussing the implications of these results, drawing attention to limitations and areas worthy of future research.

Chapter 1

General introduction

1.1 Life history variation and its importance in ecology and evolution

The fact that different organisms follow different sequences of events between birth and death has long been apparent, and the sequence of age-specific survival probabilities and reproduction that an organism exhibits under natural conditions is commonly referred to as its life history (Partridge et al. 1991). Life history theory is the area of evolutionary biology concerned with understanding the evolutionary processes that lead to organisms maximising their reproductive success (Stearns 2000), and explaining the life history variation apparent in nature (Stearns 1977).

Life-history variation is evident at multiple levels of biological organisation, though the diversity is particularly pronounced among species. Much work has focused on explaining the so-called fast-slow life history continuum (Stearns 1983), with some suggesting that this continuum arises from adaptation to varying environments that differ in their mortality schedules (Stearns 1977; Promislow and Harvey 1990). However, recent work has shown that the fast-slow continuum is likely an oversimplification given that in some cases life-histories are best defined by more than a single axis and that the traits defining the fast-slow continuum show little consistency across taxonomic groups (Bielby et al. 2007; Jeschke and Kokko 2009). Although differences at the species level are particularly pronounced, there is also substantial variation among individuals of the same species. For example, Ardia (2005) used brood manipulations to show that tree swallow (*Tachycineta bicolor*) populations at different latitudes exhibited different life history strategies. They showed that individuals from populations at low latitudes maintaining immune function and failing to increase reproductive expenditure into enlarged broods, whilst individuals at high latitudes increased reproductive investment, thereby maintaining offspring quality in enlarged broods, but mounted weaker immune responses. Similarly, Morrison and Hero (2003) showed that amphibian populations at high altitudes and latitudes tend to be larger, reach maturity later, and have fewer clutches.

Life-history variation among individuals belonging to the same population is also ubiquitous, forming the raw material for adaptive phenotypic evolution. For example, growth (Festa-Bianchet et al. 2000; Russell et al. 2002), age at first reproduction (Hadley et al.; Fay et al. 2016), reproductive lifespan (von Holst et al. 2002; Bouwhuis et al. 2010), and fecundity (Hewison and Gaillard 2001), amongst many other traits, are known to vary between individuals in wild populations. Understanding the causes of between-individual life-history variation remains a key goal in evolutionary ecology due to its importance for population and evolutionary dynamics. For example, there has been much development regarding methods to incorporate individual life-history variation into models of population dynamics (Benton et al. 2006), with such studies illustrating that individual variation can influence population growth (Bjørnstad and Hansen 1994; Pfister and Stevens 2003), equilibrium density (Bjørnstad and Hansen 1994), and population variability (Lindström and Kokko 2002; Beckerman et al. 2002). Furthermore, life-history differences between individuals are important, if genetically derived, for enabling adaptation to changing conditions (Jager 2001), and have been implicated in the evolution of a variety of traits including cooperative breeding (Hatchwell and Komdeur 2000) and animal personality (Wolf et al. 2007; Biro and Stamps 2008).

1.2 What do we know about the causes of reproductive variation?

Reproduction is a complex aspect of an individual's life history, and the reproductive success of free-living individuals can vary substantially (e.g. Kruuk et al. (1999); Wauters et al. (1995)). This variation in individual reproductive performance is very important from an evolutionary perspective, given that the way an individual reproduces influences its contribution to future generations, making it a key component of Darwinian fitness (Stearns 1976). Studying reproductive variation in unmanaged populations is particularly vital because the individuals that make up these populations tend to harbour genetic diversity that has been less influenced by human intervention, experience a wide range of

environmental conditions, and are therefore exposed to a greater variety of selection pressures. As a result, studies conducted using natural systems are particularly vital for understanding the causes of the reproductive variation apparent in nature, as well as discerning the consequences of such variation for eco-evolutionary dynamics (Pelletier et al. 2009; Vindenes and Langangen 2015). Such understanding is likely to prove useful in applied settings, such as maintaining ecosystem function in the face of mounting pressures from human-driven environmental change (Weese et al. 2011; Alberti 2015).

1.2.1 Intrinsic differences and individual phenotype

Reproduction consists of a multitude of events that range from gaining a mate through to provisioning offspring with food after birth or hatching. As a result, variation in individual reproductive success can result from differences in any number of reproductive traits that together define reproductive performance. There is a considerable body of research surrounding reproductive variation, which has revealed the importance of a number of different factors in explaining reproductive differences between individuals, in a number of reproductive traits across a variety of species (see examples below).

Genetic variation is likely to be a key source of between-individual differences in reproductive traits, but it can be difficult to study in natural populations as the quantitative genetic methods used to do so require large amounts of phenotypic data from many individuals of known relatedness. Nevertheless, studies have provided significant heritability estimates for traits including age at first reproduction (Charmantier et al. 2006), clutch size (Christians 2002), and maternal yolk hormone transfer (Tschirren et al. 2009). Age is arguably one of the most studied sources of variation in reproductive traits among same-sex individuals belonging to the same population. For example, studies have illustrated age-related variation in traits including the timing of parturition (e.g. Lunn et al. 1994) or egg laying (e.g.González-Solís et al. (2004); McCleery et al. (2008)), offspring number (e.g. Ericsson et al. (2001); McCleery et al. (2008); Wilson et al. (2009)), offspring size (e.g. Lunn et al. (1994); Ericsson et al. (2001); Wilson et al.

(2009)), offspring sex ratio (e.g. Blank and Nolan (1983); Côté and Festa-Bianchet (2001b), but see Hewison and Gaillard (1999), and weaning or fledging success (e.g. Lunn et al. (1994); Ericsson et al. (2001); Beamonte-Barrientos et al. (2010)). There has also been interest into the effects of experience on the patterns of individual reproduction. For example, both male and female Seychelles warblers (*Acrocephalus sechellensis*) showed improved reproductive performance if they had already bred at least once, which in females is mediated through improved nest construction and longer time spent incubating, and in males is mediated through improved clutch defence (Komdeur 1996). Similar effects of breeding experience on reproductive traits have been shown for a variety of species, including western gulls (*Larus occidentalis*) (Pyle et al. 1991), Antarctic fulmars (*Fulmarus glacialoides*) (Weimerskirch 1990), and northern elephant seals (*Mirounga angustirostris*) (Sydeman et al. 1991).

Ample work has also focused on the role of individual phenotypic differences, which are likely to be partially genetically determined, in mediating between-individual variation in reproductive traits. Body size is a key determinant of reproductive success in both males and females of many species, because it can influence a variety of factors, including the resources available for reproduction and competitive performance. Consequently, body size (or body mass in numerous studies) has received significant interest as a possible source of between-individual variation in reproduction. Body size has been shown to be an important predictor of male mating success in many species due to its effects on social rank or competitive ability(Schuett 1997; Lidgard et al. 2005; Alonso et al. 2010). Other studies have uncovered more subtle effects of male body size, illustrating associations between male size and other aspects of reproduction, such as offspring sex ratio (Kolliker et al. 1999). Body size has also been shown to be an important explanatory variable in studies on multiple traits in females, such as the probability of reproduction (Jorgenson et al. 1993), fecundity (Sand 1996; Albon et al. 2017) or potential fecundity (Hewison and Gaillard 2001), offspring size/growth (Birgersson and Ekvall 1997; Côté and Festa-Bianchet 2001b; Oftedal et al. 2001), and

offspring survival (Campbell and Slade 1995; Clutton-Brock et al. 1996; Jones et al. 2005), just to name a few. However, body size may not always explain variation in reproductive success, particularly once variation in lifespan has been accounted for, because larger individuals may be more likely to reach old age (Gaillard et al. 2000). Similarly, the effect of variation in male secondary sexual characteristics on mating success have been studied for many years (Thusius et al. 2001; Preston et al. 2003; Stein and Uy 2005), providing profound insights into sexual selection. More recently, studies have begun to ask how other aspects of the phenotype, that are less frequently measured in wild individuals, influence individual reproductive expenditure, such as the resistance to oxidative stress (Bize et al. 2008) and personality (Cole et al. 2012; Cauchard et al. 2013).

1.2.2 The role of the environment

An individual's phenotype derives from a combination of its genotype, the environment it experiences, and genotype-environment interactions (which result in a single genotype giving rise to different phenotypes under contrasting environmental conditions (Lynch and Walsh 1998)). Therefore, environmental conditions, such as population density, weather, and food availability, will often have a role to play in generating variation in reproductive expenditure by influencing aspects of the phenotype, such as body size. Studies surrounding the effects of environmental change on individual reproduction can be broadly grouped into those that have investigated immediate responses to changes in environmental conditions and those examining delayed effects of conditions experienced at a particular point in an individual's life.

Conspecific population density and weather variables have received the most attention, both when examining variation over the short- and long-term. For example, greater conspecific density has been linked to changes in many components of reproduction, including laying/parturition date (Arcese et al. 1988; Eccard and Ylönen 2001), clutch size in birds (Arcese et al. 1988; Wilkin et al. 2006), and the number of

offspring reaching independence (Arcese et al. 1988; Sillett et al. 2004; Wauters and Lens 1995). Similarly, temperature and rainfall in specific periods have been associated with short-term variation in reproductive traits. For example, wild boar (*Sus scrofa*) are more likely to reproduce when temperature and rainfall were low during the spring and high over the summer (Servanty et al. 2009). Likewise, high autumn rainfall has been associated with delayed calving in red deer (*Cervus elaphus*) on the Isle of Rum, Scotland (Nussey et al. 2005), whilst blue tits reduce their clutch size when ambient temperatures are high (*Cyanistes caeruleus*) (Haywood 2008). When it comes to longer-term effects of the environment, variation between years, in terms of both population density and weather conditions, induce substantial inter-cohort variation in the reproductive success of both males (Gaillard et al. 1997; Rose et al. 1998) and females (Albon et al. 1987; Gaillard et al. 1997; Forchhammer et al. 2001), as a result of variation in traits such as the age at maturity (Albon et al. 1987; Gaillard et al. 1997; Forchhammer et al. 2001), survival (Gaillard et al. 1997; Rose et al. 1998; Forchhammer et al. 2001), and fecundity (Albon et al. 1987; Forchhammer et al. 2001).

A substantial amount of research has examined the influence of variation in the resources used by wild individuals on reproductive traits, largely because food availability is generally expected to be a key determinant of reproductive success (Martin 1987; Boutin 1990). The majority of this work is conducted on birds, likely due to their suitability for food supplementation experiments. Studies using such supplementation regimes, and to a lesser degree using natural variation in resource quality or quantity, have shown the importance of food availability for individual reproductive success. For example, food availability correlates with clutch size (Korpimäki and Hakkarainen 1991; Haywood and Perrins 1992), laying date (Arcese et al. 1988; Hörnfeldt and Eklund 2008), nestling weight (Arcese et al. 1988; Naef-Daenzer and Keller 1999), and the number of breeding attempts (Arcese et al. 1988; Nagy and Holmes 2005). Fewer studies are conducted on wild individuals from other taxonomic groups, with mammalian species having received the most attention after birds. Food supplementation experiments on

mammals have provided evidence for an important role of food availability in reproductive performance (Boutin 1990). For example, Arctic ground squirrels (*Spermophilus parryii*) subject to food addition were more likely to lactate, had offspring with faster growth rates, and were more likely to successfully wean their litter (Karels et al. 2000). Similarly, tropical mouse females (*Peromyscus mexicanus*) provided with additional food start breeding earlier, have more successful breeding attempts, and wean more offspring (Duquette and Millar 1995). Many studies attempting to understand the effects of natural variation in resource availability use population density as a proxy, but a small number have been able to quantify natural variation in food availability when studying mammalian reproduction. For example, variation in spruce cone abundance between-years and/or between territories has been linked to the probability of reproduction (Wauters and Lens 1995), offspring growth (Humphries and Boutin 2000), and offspring survival (Wauters and Lens 1995; Humphries and Boutin 2000) in the American red squirrel (*Tamiasciurus hudsonicus*).

1.3 The importance of movement ecology to studies of reproductive variation

Because individual reproductive effort is expected to vary given individual body condition (McNamara and Houston 1996), the reproductive decisions made by individuals are likely to be at least partially based on the resources available to them. Because an individual's access to heterogeneously distributed resources is determined by its space use, understanding how differences in the way individuals use space, and the effect that this has on their access to resources, will be important for understanding variation in reproduction. Indeed, recent studies have drawn attention to the likely importance of individual space use in linking environmental conditions to variation in survival, reproduction, and therefore population dynamics (Mobaek et al. 2009; Morales et al. 2010).

Studies examining the role of resource variation, occurring at relatively large spatial

scales, such as at the population level (e.g. Humphries and Boutin 2000) or for plots containing multiple individuals (e.g. Lambrechts et al. 2004), provide a useful starting point for understanding how variation in resource availability influences reproductive expenditure. However, there has been little attempt to characterise resource variation at spatial and temporal scales more relevant to the individual (but see Saether and Heim 1993, Wauters and Lens 1995, and Seki and Takano 1998), despite the fact that individuals are more likely to adjust their reproduction to variation in the resource levels they actually experience, rather than to variation in the resources available to the population as a whole. Furthermore, it is evident that individuals often vary substantially in their space use. For example, studies within movement ecology find that individuals belonging to the same population can vary markedly in many aspects of their movement, including in their dispersal (Bowler and Benton 2005), migratory strategies (Chapman et al. 2011), and in their home ranges (van Beest et al. 2011b).

The home range concept is commonly used to describe the space use of individuals, with home ranges being traditionally defined as "that area traversed by an individual in its normal activities of food gathering, mating, and caring for young" (Burt 1943). This definition clearly suggests an intrinsic link between space use and reproduction, but very little work has estimated the space use of wild individuals, such as home ranges, and examined how between-individual differences in space use patterns influence components of fitness, such as reproduction. Indeed, this disconnect between knowledge on animal movement, and understanding its consequences for variation in fitness, has been cited as a challenge for future research (Hebblewhite and Haydon 2010). It has also become apparent that incorporating information on space use may be essential for understanding how genetic differences between individuals contribute to reproductive variation. The field of quantitative genetics has made it possible to estimate the contribution of genetic differences between individuals to the total variation in complex traits in wild populations, when relatedness between the individuals belonging to these populations is known. The quantitative genetic approach uses the premise that if a trait is to some

degree genetically determined, then relatives, because they share genes, will be more similar in their phenotype (Falconer and Mackay 1996; Lynch and Walsh 1998). One complication is that when relatives also experience similar environmental conditions, their phenotypic similarity can derive from shared genes or shared environment effects (Kruuk and Hadfield 2007). Many organisms exhibit natal philopatry, where individuals stay in (or return to) the area where they were born. When this is the case, relatives will often be clustered in space, and are likely to be exposed to more similar environmental conditions. Failing to distinguish between similarity caused by shared environments rather than shared genes can lead to biased estimates of a trait's genetic basis because we make the mistake of assuming that their similarity is caused by shared genes alone. Therefore, estimating the space use of individuals within long-term studies may prove invaluable when investigating the genetic basis to parental care variation in natural systems.

The scarcity of cases where individual space use has been incorporated into studies of reproductive variation may be caused by the somewhat divergent research foci within the fields of movement ecology and evolutionary ecology, and the effect that this divergence has on the data that are routinely collected. Movement ecology has been instrumental in developing technology and analytical tools that are rapidly advancing the abilities of scientists to understand the determinants of animal movement. For example, the development of Global Positioning System (GPS) technology has drastically increased the spatial and temporal resolution of animal tracking data, making it possible to examine the causes and consequences of movement in even the most cryptic of species (reviewed in Cagnacci et al. (2010)). However, a downside of such advances is that it is prohibitively expensive to employ such technology on large numbers of individuals. As a result, such studies provide very detailed information on individual space use for a relatively small number of individuals, but often lack the detailed data on individual vital rates necessary to associate this movement data with variation in fitness or its components. On the other hand, studies of evolutionary ecology in the wild often record life-history data from large numbers of individuals that have been followed throughout their lives, but such studies

are forced to use proxies of resource availability or supplementation experiments in order to understand the effect of differences in food availability. In many cases, this limits the ability of such studies to draw substantial conclusions about the role of resource availability in mediating between-individual fitness differences. Consequently, it is now essential to find ways to combine approaches from movement ecology and evolutionary ecology to understand how differences in space influence individual survival and reproduction, and how this plays into population and evolutionary dynamics. This gap in the current literature was a key motivating factor for this thesis.

1.4 The need for more studies of parental care in the wild

Parental care is a key component of reproductive expenditure in many species, and is crucial to reproductive success, as it often involves pronounced energetic inputs from parents and is key for offspring survival to recruitment. For example, in mammals, where care is usually provided by the female only, lactation (rather than other components, such as gestation and defence of offspring) is the most energetically costly part of reproduction for mothers (Clutton-Brock et al. 1989) and offspring are unable to survive without the nutrition provided by their mother during early development. Parental care can be defined as any parental trait that increases the fitness of offspring, and that originated for or is currently maintained for this purpose (Smiseth et al. 2012). An individual's investment into parental care can be one of the most difficult aspects of reproduction to study in the wild. A key reason for this is that it is often difficult to observe care because parents are elusive and/or offspring are cared for in a den or nest. It is also difficult to record detailed behavioural data on large numbers of individuals because such data collection often requires many hours of observation on each parent and its offspring. As a result, when it comes to understanding reproductive variation in natural systems, we are particularly limited in our understanding of the sources of between-individual variation in parental care. This limitation is more pronounced for some taxonomic groups than others. Although mammals have received more attention than some other groups such as

reptiles and amphibians, much of the work investigating parental care variation in the wild has been on birds (Stahlschmidt 2011). This is likely because they are amenable to experimental procedures, such as supplementary feeding, handicapping, and brood size manipulations, and can, in many cases, be encouraged to use artificial nestboxes, which makes the monitoring of parental care behaviour substantially more straightforward.

There has been relatively little work to understand parental care variation in nature within non-avian taxa and without the use of experimental manipulation. This is a substantial limitation when it comes to understanding the causes and consequences of variation in reproductive effort because many species do not exhibit the biparental care so prevalent in birds, and food supplementation is unlikely to provide much insight into the effect of natural variation in resource quantity/quality. Work conducted on birds has provided insights into some of the sources of variation in the care provided by parents that is apparent in the wild. We now know that parents adjust their care behaviour according to a diverse range of factors, including their age (Daunt et al. 2001; Beamonte-Barrientos et al. 2010) and breeding experience (Limmer and Becker 2009; Byholm et al. 2011), weather conditions (Delia et al. 2013; Öberg et al. 2015), predation risk (Fontaine and Martin 2006; Ghalambor et al. 2013), and the social environment, including brood size (Hegner and Wingfield 1987; Sanz and Tinbergen 1999), partner performance (Hinde 2005; Harrison et al. 2009) and the number of helpers (Bales et al. 2002; Paquet et al. 2013). Nevertheless, we still do not have a good grasp on the importance of such factors in determining the care provided by parents from other taxonomic groups, and, in particular, little is known about how individual investment into parental care is affected by individual space use and genetics.

The environmental conditions experienced by a parent are expected to alter the costs to the parent of providing parental care and/or the benefits of care to offspring, and are thereby expected to influence parental care provisioning (Clutton-Brock et al. 1991). Although research has investigated the relationships between parental care and a variety of environmental components, including resource availability (e.g. Rachlow and Bowyer

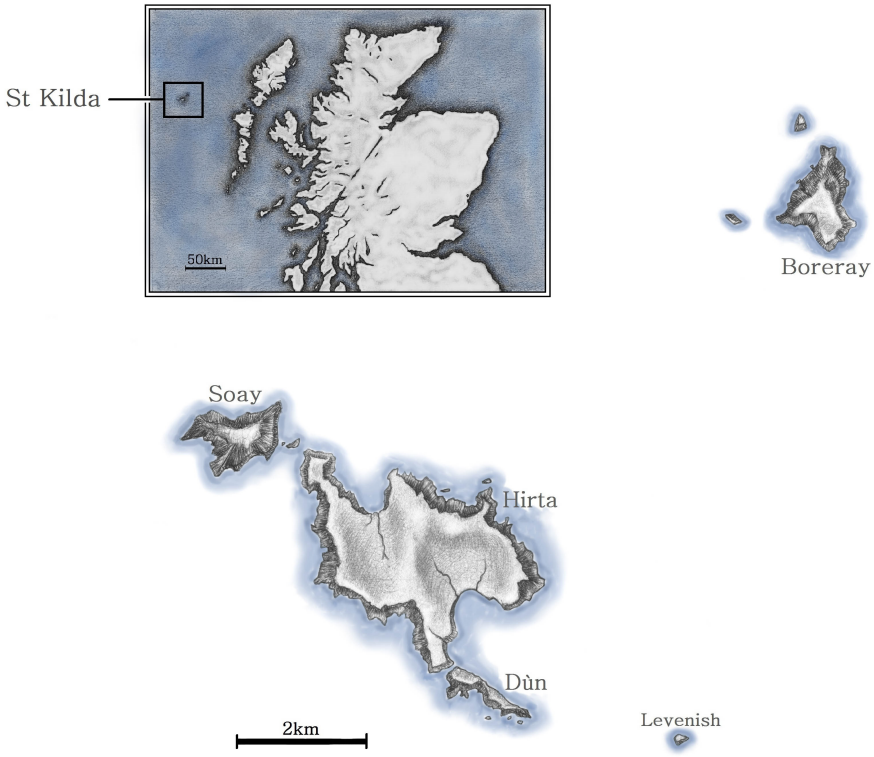
(1994); Whittingham and Robertson (1994); Andrews et al. (2016)), little work has examined the associations between space use and parental care. This is despite the fact that individuals must use space in a way that gives them access to all the resources necessary to grow, survive and reproduce. Likewise, studies examining the genetic component of parental care variation in natural populations are rare (but see Freeman-Gallant and Gothstein (1999); MacColl and Hatchwell (2003b); Tschirren et al. (2009); Dor and Lotem (2010); McGaugh et al. (2010)), but such understanding is important for discerning how care evolves under natural selection, and for improving production and welfare traits in animal agriculture. The lack of research probably stems from the difficulty of collecting high volume data on parental care, particularly in the case of behaviour. As such, alternative approaches are needed to investigate the genetic basis of parental care in wild populations.

1.5 The study population: St. Kilda Soay sheep

This thesis uses data from the feral population of Soay sheep (*Ovis aries*) on the island of Hirta in the St. Kilda archipelago, Scotland (see Fig. 1.1). Soay sheep are small (on average adult females weigh around 24 kg in August, whilst adult males weigh around 38 kg (Campbell 1974; Clutton-Brock et al. 1996)), horned sheep that are believed to be the remnants of primitive domesticated sheep introduced to the British Isles in the Bronze age (Clutton-Brock et al. 2004) (see Fig. 1.1). In 1932, 107 Soay sheep were brought to the island of Hirta from the neighbouring island of Soay, following the evacuation of the human population and the removal of their livestock (Clutton-Brock et al. 2004). Since their introduction, Soay sheep on Hirta have been left entirely unmanaged, and the island is now home to between 600 and 2300 sheep, depending on variation in mortality between years. Due to the lack of predators and competitors, the population is food-limited and shows periodic population crashes in which up to 70% of animals on the island die (Clutton-Brock et al. 2004). These crashes are caused by a combination of population density, weather conditions, and the age- and sex-structure of the population (Coulson

et al. 2001).

Scientific study of the sheep on Hirta commenced in the 1950s (see Jewell 1974); however, the long-term individual-based study that continues to this day, and has provided much of the data for this thesis, began in 1985. The current St. Kilda Soay sheep project focuses on the 170 hectare portion of the island known as Village Bay (total island size is 638 hectares) that is home to approximately 30% of the total island population (Clutton-Brock et al. 1992). This area contains two broad vegetation types. The first, which is known as the 'inbye', consists of grassland present on the ground previously cultivated by the human population, whilst the second, known as the 'outbye', consists of heather-dominated (*Calluna vulgaris*) moorlands (Gwynne et al. 1974). Study of the sheep on Hirta relies on individuals being marked shortly after birth, or at their first capture, with plastic ear tags, and more than 95% of sheep residing in the study area are now tagged and are therefore individually identifiable (Clutton-Brock et al. 1992).



(a)

(b) (c)

Figure 1.1: St. Kilda Soay sheep are found on the islands of Soay and Hirta in the St. Kilda archipelago, Scotland (a; drawing by Becky Holland). The long-term individual based study focuses on the population within the Village Bay area of the island of Hirta (b). Soay sheep are small, horned sheep, and 95% of the Village Bay population have been given plastic ear tags to make it possible to track individual life histories (c).

Field work for the St. Kilda Soay sheep project involves three key periods of data collection in each year that coincide with key periods in the sheep life cycle (Fig. 1.2). The first occurs in March-May, starting at the end of the peak over-winter mortality and including the majority of lambing. Most adult females conceive each year, and the likelihood of juveniles conceiving in their first year of life is related to their body weight (Clutton-Brock et al. 2004). Adult females can bear either singleton or twin litters, and twinning rate is also dependent on body weight (Clutton-Brock et al. 2004). Soay lambs develop rapidly, beginning to ingest grass at around one week of age (Clutton-Brock et al. 2004). During lambing, females are monitored for parturition and within a few days of birth, lambs are tagged. When lambs are captured, a variety of data are taken, including morphometric measurements, such as body mass, and samples of blood and tissue that are used for genotyping. This information is then used to construct the pedigrees/genomic relatedness matrices necessary for quantitative genetic analysis. Individuals that are not caught at birth are sampled when captured in subsequent trips or during necropsies. The second trip takes place in July/August, as lambs are becoming fully nutritionally independent, and its primary aim is the capture of as many Village Bay sheep as possible. More than 50% of the population are caught each year and the processing of each individual provides a variety of information, including data on body mass. The third expedition to the island occurs in October/November to coincide with the mating season, otherwise known as the rut. At this point females are monitored for oestrus and untagged males that enter the study area are immobilised, tagged, measured, and sampled, so that they can be incorporated into the pedigree.

During each of the three trips to the island, ten censuses of the whole study area are conducted. Each census occurs in a single day and involves three fixed routes being walked simultaneously to cover the entirety of Village Bay. The identity of all individuals observed is noted, and their grid reference is recorded to the nearest 100 m. These data make it possible to characterise individual home ranges, and the collection of vegetation data means we can derive estimates of the vegetation used by each individual. A variety

of vegetation data are available. Grazing exclosures provide information on sward productivity and sheep offtake and samples taken from five permanent transects covering Village Bay provide estimates of the biomass and species composition of plant communities. In terms of this thesis, the most important vegetation data are the plant percentage cover scores for each hectare. Village Bay has been divided into 160 one hectare squares, and between 2008 and 2012 each hectare was surveyed to obtain both a list of all vascular plant species present and ocular estimates of the percentage cover of each species (to the nearest 5%).

The fact that the Soay sheep system provides identifiable individuals that can be followed in the field throughout their lives, detailed life-history and phenotype data, the spatial data necessary to characterise individual space use, and pedigree information, makes this population an ideal system for studying the genetic and environmental determinants of variation in reproductive effort, and in particular maternal care.

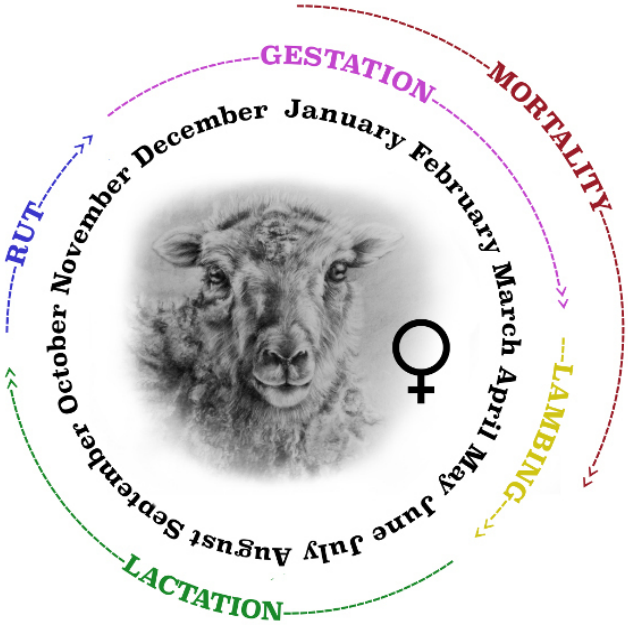


Figure 1.2: Soay sheep rut in autumn, at which time most adult females conceive. Peak mortality occurs over the winter, with most sheep dying of malnutrition. Females give birth in April or May, either to a singleton lamb or to twins. They then provide milk to their lambs during the summer, though sucking bouts are short and infrequent by the time the summer catch comes around in August (Drawing by Becky Holland).

1.6 Objectives

The principle aim of this PhD was to understand how differences between female Soay sheep, in terms of their space use and therefore their access to high quality vegetation, and their genetics, influence the care they provide to their lambs, both before and after birth. In Chapter 2, I provide details of a field-based behavioural study conducted on 69 mothers and their lambs to understand how a mother's home range quality influenced her care behaviour and the behaviour of her lamb over the maternal care period. I did this by selecting females whose home ranges contained either a high or low proportion of *Holcus lanatus*, a grass that is characteristic of a key high quality grassland community, that were then observed multiple times between the birth of the lamb in April and weaning in August. In Chapter 3, I used existing data from the long-term study to understand if a female's access to high quality vegetation (again *H. lanatus*), in combination with age, body mass, population density, and winter severity, influenced the costs experienced as a result of reproduction, both in terms of survival and future reproduction. In Chapter 4, I used information on individual locations to explore methods of accounting for shared environmental effects among relatives in quantitative genetic analyses of lamb and adult traits, due to the natal philopatry exhibited by female Soay sheep. These models were then used in Chapter 5, where I investigated the potential role of genetic differences between females in generating maternal care variation. To do this, I conducted another field behaviour study where females were selected based on their estimated genetic merit for lamb growth, and were then observed, alongside their lamb, to understand if there was any association between this estimated genetic merit for lamb growth and the maternal and lamb behaviours recorded. Finally, in Chapter 6, I present a general discussion of the findings of this thesis, relating them to the existing literature, and finishing with future directions for research aimed at understanding the causes and consequences of variation in reproductive expenditure in wild animal populations.

Chapter 2

Female Soay sheep do not adjust their maternal care behaviour to the quality of their home range

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Regan CE, Pilkington JG, Smiseth, PT. 2017. Female Soay sheep do not adjust their maternal care behaviour to the quality of their home range. Behav Ecol. 28:962-973.

2.1 Abstract

Resource availability, through its impact on the costs and benefits of parental care, is expected to influence parental care behaviour. There has, to our knowledge, been no attempt to understand how variation in the resource use of wild individuals influences individual parental care behaviour. To understand how natural resource variability affects maternal care in female St. Kilda Soay sheep, we selected 69 females whose home ranges varied in quality (measured as the mean percentage cover of *Holcus lanatus*), and recorded the behaviour of each individual and her lamb over the period of maternal care. Home range quality did not influence suckling or non-suckling behaviours of the female or her lamb, suggesting that maternal care did not vary with a female's access to resources. Growth rate analyses confirmed the behavioural results, with no association between home range quality and the weight gain of lambs between birth and weaning. This work suggests that female Soay sheep faced with poorer resources do not favor their own future success over that of their lamb, and thereby do not exhibit a conservative reproductive strategy. This may be because when resource levels are high during the summer, females are able to offset the costs of lactation by consuming additional resources, regardless of the location of their home range. Our results suggest that more studies characterizing the environment experienced by individual animals will be necessary to fully understand how individuals alter their behaviour in response to temporal and spatial variation in the environment.

2.2 Introduction

Parents of many species provide their offspring with parental care, which can be defined as any parental trait that increases the fitness of the offspring, and that originated for or is currently maintained for this purpose (Smiseth et al. 2012).

Providing care often comes at a cost to the parent's own survival and future reproduction, at which point it can be termed parental investment (Smiseth et al. 2012). To maximise their own lifetime reproductive success, parents must balance the benefits of investing in current offspring against the costs of reduced future reproductive opportunities. As a result, parents are expected to adjust the level of care they provide to the benefits of care to their offspring and the cost to themselves (Winkler 1987). Many factors have the potential to influence the relative costs and benefits of parental care thereby contributing to variation in the level of parental care. These factors can relate to the offspring themselves, for example their relatedness to the parent (Møller and Birkhead 1993; Dixon et al. 1994) or their sex (Hasselquist and Kempenaers 2002). Similarly, in species where care is shared among multiple individuals, the benefit can vary depending on the amount of care provided by the focal parent as well the amount provided by its partner (Lessells 2012) or any helpers (MacColl and Hatchwell 2003b). The environmental conditions that a parent experiences can also alter the benefits of care to offspring and/or the costs of providing care to the parent, and thereby influence the level of parental care provided (Clutton-Brock et al. 1991).

The environment an individual experiences is complex, composed of a wide variety of biotic and abiotic factors. Research has shown that parental care behaviours are influenced by an array of environmental components, from predation risk (Fontaine and Martin 2006; Huang and Wang 2009) and the social environment (Bales et al. 2002; Russell et al. 2008; Brouwer et al. 2014) to weather conditions (Thierry et al. 2013; Öberg et al. 2015) and resource availability (Scornavacca et al. 2016). Much of the literature on the effects of environmental variation has focused on resource availability, which is unsurprising given that resource availability dictates the amount of energy that is available for growth, survival, or reproduction. However, empirical work is yet to uncover a consistent relationship between resource variability and parental care. Many studies report no

influence of resource availability on parental care decisions (e.g. Whittingham and Robertson 1994, Andrews et al. 2016), whilst other studies find reductions (e.g. Whittingham and Robertson 1994), or increases in parental care with increased resource availability (e.g. Rachlow and Bowyer 1994; Wong and Kölliker 2012; Markman et al. 2002). The diversity evident in the existing literature may derive from differences in the effect of resource variation on the survival and reproductive value of adults versus offspring (Clutton-Brock et al. 1991). Decreased resource availability is expected to result in increased parental care if the parent's potential for reproduction in the future is low relative to that of the offspring (Clutton-Brock et al. 1991). However, if future reproduction of the parent is less affected by resource scarcity than the future reproduction of the offspring, then a decrease in resource availability should be associated with reductions in care because parents should favour their own future reproduction (Clutton-Brock et al. 1991). This argument suggests that the effect of resource variation on parental care is linked closely with life history. For example, females of long-lived iteroparous species, such as ungulates, might adopt a conservative reproductive strategy, such that when faced with resource scarcity they allocate fewer resources to their offspring and maintain their own condition (Martin and Festa-Bianchet 2010). This is because their fitness is more dependent on their own survival than their reproductive success in any single year (Gaillard and Yoccoz 2003).

Despite the long-established interest in the effect of resource availability on parental care, there are still substantial gaps in our understanding. First, much of the previous research has utilised bird systems. Most birds have bi-parental care (Clutton-Brock et al. 1991), which is a rare pattern of care in most other taxa, including mammals. In most non-avian taxa, a single parent (usually the female) provides all care to the offspring (Stahlschmidt 2011). Where both parents provision the offspring, the response of one parent to environmental conditions may be conditional on the behaviour of the other parent (Lessells 2012), which could

make it difficult to detect an association between environmental conditions and parental care. Second, supplementation experiments are commonly used to understand how resource availability affects parental care. Such experiments might come at a cost in terms of loss of biological realism and therefore it may be beneficial to complement the use of experimental manipulations with studies using natural variation in resources. Third, the limited number of studies on naturally occurring variation in resources in wild populations are often based on comparisons between different populations (e.g. Tremblay et al. 2004). This practice is problematic because it is difficult to separate the effects of environmental conditions from behavioural differences between populations due to genetic differentiation (Johannesson and Johannesson 1996). Fourth, care must be taken to quantify environmental conditions in a way that accurately reflects its impact on the study organism. Much of the literature has focused on the effect of between-year variation in resource availability on parental investment, using population density and/or mortality as a proxy for resource availability (e.g. Robertson et al. 1992). This approach does not account for the fact that individuals are more likely to respond to the resource levels they experience in their home range than to the resources available to the population as a whole. Movement ecologists have developed sophisticated methods to estimate individual space use (e.g. kernel density home range estimators), making it possible to examine the effects of fine-scale resource variation on individual parental care decisions. However, to our knowledge, these approaches have not been used to study the effect of resource variation on parental care. Finally, studies tend not to record the behaviour of the offspring. However, any influence of environmental conditions on offspring behaviour may influence the parent's behaviour, thereby potentially influencing any relationship between parental behaviour and environmental variation such as resource availability.

The St. Kilda population of Soay sheep is an ideal system in which to study the effect of resource variation on parental care behaviour. The long term data

available (Clutton-Brock et al. 2004) make it possible to quantify both between-individual and between-year variation in environmental conditions. Furthermore, individuals are marked with unique ear tags, making it possible to record the behaviours of specific females and their lambs. Body weight is associated with many aspects of female reproduction and survival in Soay sheep, influencing the probability of conception in the first year, the likelihood that females bear twins, and the probability of over-winter survival (Clutton-Brock et al. 2004). A female's body weight is also closely tied to the birth weight of her lambs (Clutton-Brock et al. 2004), which in turn affects their early survival (Jones et al. 2005). Body weight and condition are likely to be closely related to home range quality, and there is marked variation in forage quality and quantity across the study area (Coulson et al. 1999; Regan et al. 2016). *Holcus-Agrostis* (HA) grassland is the most productive plant community on the island (as determined using grazing exclosures), containing the highest live standing-crop biomass (Crawley et al. 2004). This community is also highly palatable to the sheep, with sheep selecting for this community even at high density (Jones et al. 2006). The aim of this study is to understand how natural variation in resource availability affects patterns of maternal care in female St. Kilda Soay sheep (*Ovis aries*). To this end, we studied the parental behaviour of females and the sucking behaviour of their lambs over the period of maternal care in 2014 and 2015. We selected females based on the quality of their home range, measured as the mean percentage cover of *Holcus lanatus* (one of the dominant species in *Holcus-Agrostis* grassland) within their core home range, before following them in the field after the birth of their lambs in April/May until weaning in August.

2.3 Methods

2.3.1 Study population

Soay sheep were introduced to the island of Hirta in 1932 from the neighbouring island of Soay in the St. Kilda archipelago, Scotland (57°49° N 08°34° W). Since their introduction they have been entirely unmanaged, and the total island population now ranges from 700 to 2300 individuals, depending on variation in mortality between years. Hirta's sheep have been studied since the early 1960s, but intensive study of the Village Bay population (containing ∼30% of the total island population) commenced in 1985. To enable identification individual sheep are marked with plastic ear tags shortly after birth and within the Village Bay area more than 95% of animals are tagged (Clutton-Brock et al. 2004). A combination of mortality checks and censuses enable the monitoring of individual survival, whilst also providing information on individual space use. Female Soay sheep are philopatric, with more than 80% remaining in their natal heft throughout their life (Coltman et al. 2003). Given the home range fidelity exhibited by female Soay sheep and the substantial spatial heterogeneity in grazing quality across the study area, individuals vary in their access to resources (Regan et al. 2016) and consequently will likely vary in their reproductive investment decisions.

2.3.2 Home range estimation and animal selection

Researchers from the Soay sheep project travel to St. Kilda three times per year (April-May, July-August, October-November), and conduct ten censuses of the Village Bay area during each trip. During each census, three fixed routes are walked simultaneously and the identity and grid reference (to the nearest 100 meters) of all encountered individuals is noted. In the Spring of 2014 and 2015, we extracted census observations for all females that were recorded as being alive in

the preceding census, were aged between 3 and 8 years (to exclude young and geriatric individuals due to likely differences in their behaviour), and that had at least 49 census observations in total. This is because 49 observations is the minimum number needed to reach an asymptote in core home range area when estimating lifetime home ranges, indicating that the core home range has been reliably estimated (see Regan et al. 2016 for details). We transformed these observations onto a grid, so that the most south-westerly census observation (NF091980) became (0,0) and each step on the grid represented a distance of 100 meters. Because the census procedure means that animals are assigned a grid reference to the nearest 100 meters, individuals frequently have numerous observations with identical grid references. This can cause problems when estimating home ranges using kernel methods (Tufto et al. 1996) and we therefore added a random number between -20 and 20 (representing a distance of up to 20 meters) to both the X and Y coordinates of each observation before home range estimation (see Moyes 2007 ; Stopher et al. 2012).

Home ranges were calculated using census observations from all years of a female's life prior to the observation period to maximise the number of potential study animals, and also because data were not yet available at the time of animal selection for all censuses in the year preceding observation (we have since conducted analyses using annual home range estimates/resource selection functions - see below for details). We estimated core home ranges (70% isopleth; see Regan et al. 2016 for details) using kernel density methods with the package 'adehabitatHR' (Calenge 2006) in R version 3.1.3 (R Development Core Team 2008). Use of the reference bandwidth (h_{ref}) can result in over-smoothing and consequently biased home range estimates, leading Kie (2013) to suggest a rule-based *ad hoc* method for estimating the bandwidth. This method involves sequentially reducing h_{ref} until the 95% kernel home range polygon fragments or lacuna appear, at which point the process is stopped (Kie 2013). We estimated

home ranges using both methods, finding that in many cases the home range was already fragmented when using h_{ref}, preventing any further reduction in the smoothing parameter, and that the use of the *ad hoc* bandwidth, where possible, had very little impact on estimates of the percentage cover of *H. lanatus*, and therefore did not change our results. As a result, we present analyses using home ranges calculated using h_{ref}. Though data from both 2014 and 2015 field seasons could be used for the analyses described below it must be noted that, in 2014, females were selected specifically based on their access to resources (see below), whereas in 2015 their home ranges were calculated to enable us to account for space use when selecting females based on the predicted growth of their lambs.

We quantified the variation in home range quality by characterizing the vegetation present within each individual's home range. Using the Ordnance Survey Grid, the Village Bay study area is divided into 160 one hectare squares (100 × 100 m) [the remaining 10 hectares were not surveyed for vegetation due to access difficulties and/or a lack of vegetation (some are covered by scree)]. Between 2008 and 2012 complete species lists were compiled for the vascular plants in each hectare, and the percentage cover of each species (to the nearest 5%) was scored by eye. MJC collected all botanical data so there were no between-observer sources of error. Ocular cover estimation is the only practical method for hectare-sized plots because it averages over the within-plot spatial heterogeneity. Furthermore, calibrations of visual cover estimates against biomass data in related studies has shown that the results from the two methods are strongly correlated (e.g. Allan and Crawley 2011, MJC, unpublished analysis). Plant community boundaries are the same as described in Gwynne et al. (1974), and there has been no detectable change in the botanical composition of these communities since detailed botanical recording began in 1993 (MJC, unpublished results). We obtained home range quality metrics by calculating the percentage cover of *H. lanatus* in individual core home ranges. We did this by taking a weighted mean of the percentage covers

recorded in the hectares contained within each individual's home range. The proportion of the hectare contained within the home range was used as a weight to ensure that the varying contributions of constituent hectares was taken into account.

Upon completion of both field seasons, we estimated home range quality metrics and individual resource selection functions for the year preceding behavioural observation. We focused on the year preceding observation for two reasons. First, it was not possible to assess individual space use for the precise period in which behavioural observations were conducted because space use data are only collected three times per year (April, August, and October). Therefore, to incorporate data from the April directly preceding the birth of the lamb, whilst having enough data to estimate home ranges, we used spatial data from the four census periods (April-April) preceding the observations. Second, the resources available to a female prior to lactation are likely to influence her body weight or condition and therefore may also affect her provisioning over the maternal care period (Landete-Castillejos et al. 2003). We used annual home range quality and resource selection functions to provide a more complete picture of the relationship between resource availability and maternal care by enabling us to characterise variation in access to a wider range of plant communities and making it possible to assess the impact of characterizing home range quality at a particular temporal scale. We estimated annual home ranges and home range quality metrics for each individual in the same way as the lifetime home ranges, but using only location data from the four census periods (April-April) preceding the time of observation. Because using the mean percentage cover of *H. lanatus* as a measure of home range quality may be sensitive to variation in home range size we calculated an alternative measure of quality for annual home ranges in order to assess the robustness of our results. We weighted the percentage cover of *H. lanatus* in each hectare covered by an individual's utilization distribution (70% isopleth) by the amount of the hectare

contained within the utilization distribution before summing these values to give an estimate of the area of an individual's home range that was covered by *H. lanatus*.

We also estimated individual resource selection functions for the year before each field season in order to obtain a more thorough measure of an individual's use of habitat. Resource selection functions (RSFs) estimate habitat selection by comparing the characteristics of locations used by organisms against those not used (Manly et al. 2002); however, because we are unable to explicitly ascribe absences to locations, our data correspond to a used/available design (Boyce et al. 2002). By using RSFs, we could characterise each individual's selection for multiple plant communities, including HA grassland. We estimated second-order habitat selection; that is, the selection of the home range (Johnson 1980), as this most closely corresponds to the home range quality measures described above. We sampled n used locations directly from the 95% kernel annual home range contour (calculated as above), whilst n available locations were sampled randomly from the area covered by the 160 hectares for which there are vegetation data (n was the number of census observations for each individual over the April-April preceding observation). To make use of percentage cover data for the fourteen most common plant species, but reduce the number of variables included in the RSF, we used principle components analysis to derive three variables (the first three principal components [PC1, PC2 and PC3] which accounted for 59.3% of the variation across hectares). PC1 loaded negatively on species present in *HA* grassland (including *H. lanatus*, *Agrostis capillaris* and *Festuca rubra*) and in the maritime *Festuca-Plantago* swards (including *Plantago lanceolata* and *P.maritima*) and positively on species associated with heathland, including *Calluna vulgaris* and *Nardus stricta* (see Appendix A Fig. S1). In contrast, PC2 loaded positively on species associated with HA grassland and negatively on species associated with *Festuca-Plantago* swards, whilst PC3 loaded positively on *Calluna vulgaris* (see Appendix A Fig. S2). We calculated an RSF for each female using the three

principal components as predictors in a logistic regression (Manly et al. 2002). We then extracted the coefficients from these regressions for use in subsequent models aimed at understanding how variation in resource selection was associated with variation in maternal care behaviours (see below).

2.3.3 Behavioural observations

We successfully tracked 34 females in 2014 and 35 females in 2015 (females were never observed in both years), all of which gave birth to singleton lambs. We focused on singletons because low twinning rates in both years (2014 - 18%, 2015 - 12%) meant that it was unlikely that we would be able to follow enough twins to enable us to detect any difference in the response of females to resource variation as a result of differences in litter size. The females varied substantially in the quality of their home ranges, with the mean percentage cover of *H. lanatus* in lifetime home ranges ranging from 9.6% to 61.5%. To monitor the behaviour of females and their lambs from birth until weaning, we made three trips to St. Kilda each year. The first started in mid-April and lasted until late May (2014 - 15/04 to 28/05, 2015 - 13/04 to 21/05), the second trip occurred in June (2014 - 23/06 to 02/07, 2015 - 23/06 to 05/07) and the final trip commenced in late July (2014 - 22/07 to 04/08, 2015 - 22/07 to 03/08). Focal observations were conducted once for each week of the lamb's life where possible (see Fig. 2.1 for an illustration of observation spread for each individual) using 'Animal Behaviour Pro' (Newton-Fisher 2012). One female (BR501) and her lamb died shortly after the second observation was conducted; however, the inclusion of data for this pair did not modify the results and, therefore, we present results with these data included. Individuals were located using 10x42 binoculars (Vortex, USA) and spotting scopes (16-48x; Opticron, UK), and were then observed from a distance of at least ten meters. It was not possible for observations to be done totally blind because animals were specifically selected based on their home range quality and because there are visible

differences in the vegetation across the study area; however, assistants had limited information regarding the home range quality of different animals and the quality of different communities within Village Bay. Observations were conducted between 08:00 and 19:00, and the focal watches for each individual were distributed across the day and between observers (2 per trip) to prevent any between-individual differences caused by the data collection procedure. Focal observations lasted one hour, with lamb behaviour recorded continuously and female behaviour recorded instantaneously at two minute intervals (see Table 2.1 for descriptions of the recorded behaviours). Whenever females and lambs separated, we preferentially kept the lamb in sight in order to accurately record non-sucking behaviours. Hirta is littered with dry-stone structures known as cleits, which were used for storage by the St. Kildans, but are now used for shelter by the sheep. Sheep are very difficult to observe when inside a cleit, and we therefore ended observations when both the female and her lamb entered a cleit. We continued with observations when either the female or her lamb were inside a cleit, recording them as 'Out of sight', as in this case we could be sure that no suckling events were missed. There was one case where a lamb sucked from both its mother and grandmother and in this case we recorded, but later excluded, all sucks from the grandmother prior to analysis. In total, we conducted 570 hours of observations, with between two and thirteen focal watches per female-lamb pair (Fig. 2.1).

Table 2.1: Descriptions of the female and lamb behaviours recorded during focal observations.

Individual	Behaviour	Description
Lamb	Sucking	Recorded each time the lamb was in contact with the teat. The head is usually tilted upwards slightly and sucking is often accompanied by tail wagging and intense butting of the teat. Failed suckling events were classed as periods of suckling behaviour that lasted less than five seconds. For each suckling event, termination by either the female or lamb was noted. Female termination was characterised by the female walking off or kicking the lamb, whereas lamb termination was noted when the lamb stopped sucking of its own accord.
Lamb	Grazing	Short periods of head down movement, but where lambs were explicitly seen taking bites of grass (in the first few days of life they show interest in grass but are yet to take it into their mouth).
Lamb	Resting	When the lamb is lying down.
Lamb	Playing	Either lone play or play involving other lambs, generally characterised by short bursts of running, leaping, and head butting.
Lamb	Other	A category for all behaviours that do not fit into the other described categories. It generally consists of movement behaviour.
Lamb	Out of sight	This category was used to note periods when the lamb was not in view, whether this was because the lamb was obscured by an object, had gone out of sight during play, or had been disturbed in some way.
Female	Suckle	Noted when the female's behaviour was recorded during a suckling bout.
Female	Grazing	Head down, taking bites and short periods of head down movement between bites.
Female	Resting	Female lying down and ruminating or showing no observable activity.
Female	Moving	If the female was showing any movement not associated with grazing.
Female	Other	Periods of activity that do not fit in the other described categories. Largely made up of grooming and general alertness.
Female	Out of sight	Used to denote periods when the female was not in view.

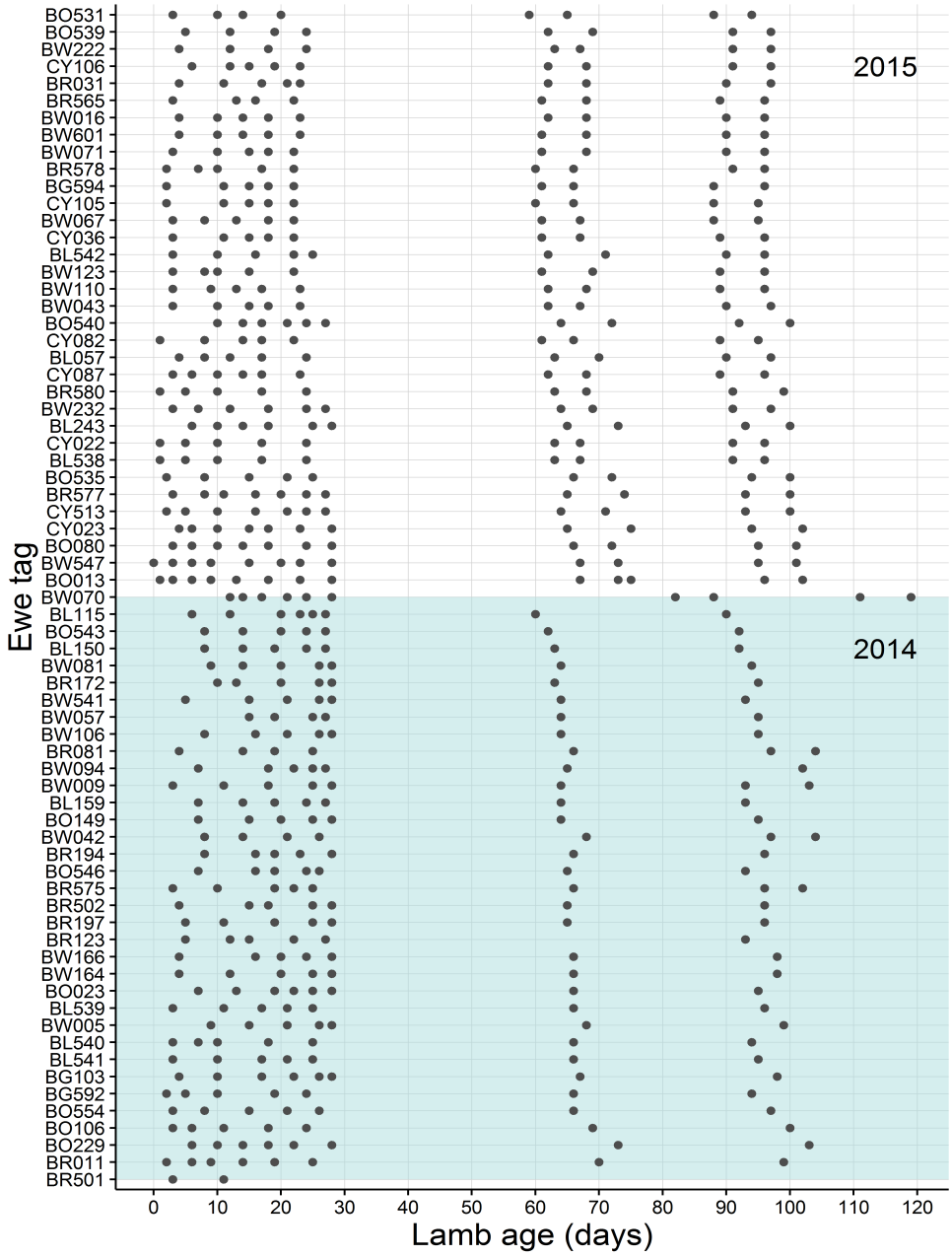

Figure 2.1: The distribution of focal observations over the 2014 and 2015 field seasons. Each field season involved three trips to St. Kilda (April-May, July-August, October-November). Female-lamb pairs were observed between two and 13 times (median = 8), with BR501 observed only twice due to mortality after the second observation. Each female was observed in only one of the two years.

2.3.4 Statistical analyses

For each focal observation, we calculated suckling frequency (the number of suckling events per hour regardless of length), total sucking time (the total time in seconds that a lamb spent sucking per hour), and the mean suckle duration (total sucking time divided by the frequency of suckling events). One suckling event which lasted 248 seconds was removed as it was a clear outlier, having likely been extended due to vigilance in response to tourist disturbance. We also calculated the frequency of failed suckling events, denoted as a suckling bout shorter than five seconds (following Hass 1990; Birgersson and Ekvall 1994; Tollefson et al. 2011) (the number of failed suckling events per hour), the frequency of female terminated suckling events (the number of suckling events terminated by the females per hour), and the total time (in seconds) that a lamb spent grazing, playing, and resting during each focal watch (grazing time, playing time, and resting time respectively). In the case of the female, we calculated the number of time points (out of 30) that she spent in each of the recorded behaviours, providing information on grazing frequency, resting frequency and moving frequency.

Data were analysd using linear and generalised linear mixed models using the packages lme4 (Bates et al. 2015) and glmmADMB (Skaug et al. 2006) in R version 3.1.3 (R Development Core Team 2008). All models included individual identity and the date on which the observation was conducted as random effects. They also included year (two level factor), maternal age (covariate) and lamb age (covariate) as fixed effects. To understand how a female's home range quality (both lifetime and annual) influenced maternal care, we compared a subset of 10 models for each trait, that contained all combinations of the following fixed effects: a quadratic term for lamb age to determine if a nonlinear relationship was a better fit to the data, the mean percentage cover or absolute cover of *Holcus lanatus* to test for an effect of home range quality, a quadratic term for the mean percentage cover or

absolute cover of *Holcus lanatus* (again to test for a nonlinear relationship), and a first-order interaction between lamb age and the mean percentage cover or absolute cover of *Holcus lanatus* to examine whether the relationship between a given behaviour and home range quality varied with lamb age. Both lamb age and the mean percentage cover or absolute cover of *Holcus lanatus* were mean centered and scaled to reduce collinearity between power terms. These models were compared using Akaike's Information Criterion corrected for small sample size (AICc). The best model was taken to be that with the lowest AICc value (Burnham and Anderson 2002); however, if there was a more parsimonious model (i.e. with fewer terms) that had a comparable AICc (<2 units difference) then the simpler model was accepted as the best model (Burnham and Anderson 2002). We present only the best model from each analysis in the results, but the outputs of full models and the AICc scores for full and best models are available in the supporting information (Appendix A Tables S1-S4).

To understand if our results were affected by density variation within the study area we re-analysd the behavioural data using annual home range quality measures as above and the number of females with overlapping home ranges as an additional fixed effect. We used Bhattacharyya's affinity (BA) in adehabitatHR (Calenge 2006) to calculate the home range overlap/similarity for every pair of females that were alive and had more than five census observations in the year preceding each observation period. We then used this information to calculate the number of individuals whose utilization distribution had a BA exceeding 0.01 (BA scales from 0-1) with the utilization distribution of each behavioural female, at which point they were classed as having overlapping home ranges. For each trait we compared a set of 20 models that contained all possible combinations of the lamb age (linear and quadratic), home range quality (linear, quadratic, and first-order interaction with lamb age), and density terms. The best model was determined using AICc, as above. The results from these analyses were not qualitatively different to those

from analyses excluding density and therefore they are presented in the supporting information (Appendix A Table S2).

We used a similar approach when conducting analyses to understand whether maternal care behaviour varied with habitat selection; however, in the place of the percentage cover of *H. lanatus*, we included PC1, PC2 and PC3. We therefore compared a subset of 54 models for each trait, that contained all combinations of the resource selection variables (PC1, PC2 and PC3), a quadratic term for lamb age, and a first-order interaction between each of the resource selection variables and lamb age. As for the analyses using home range quality metrics AICc was used to compare these models, with the best model taken to be that with the lowest AICc value unless there was a more parsimonious model with a similar AICc (<2 units difference) (Burnham and Anderson 2002). Because the estimates of resource selection functions are themselves associated with error, we wanted to understand whether this impacted the results of models performed using only the parameter estimates from the logistic regression used to estimate RSFs. To do this we used the parameter estimates and standard errors from the regressions for each individual to obtain a distribution from which we selected 100 random values. We then ran our mixed models using each of these set of values, deriving a best model from each (as above) to understand how many of these models - if any - featured any of the resource selection components.

Total sucking time (with and without failed suckling events), mean suckle duration (with and without failed suckling events), and grazing time were log transformed prior to analysis in order to ensure that the distribution of the residuals had a closer approximation to normality. These behaviours, along with resting time, were then analysed using linear mixed models assuming a Gaussian distribution. We assumed a Poisson distribution when analysing suckling frequency (excluding failed suckling events), but used negative binomial mixed models (performed in glmmADMB) for suckling frequency (including failed suckling

events), female grazing frequency, female resting frequency and female moving frequency due to the overdispersion apparent in the residuals when assuming a Poisson distribution. We assumed a binomial distribution when analysing the proportion of successful suckling events, using the 'bobyqa' optimiser to aid convergence. We do not present results for playing time and the proportion of female terminated suckling events because severe zero-inflation resulted in poor residual distributions despite all transformations and error distributions employed.

To supplement the above analyses and aid in the interpretation of our behavioural results, we also investigated the effect of a female's annual home range quality on the growth of her lambs and her body condition at the end of the summer. Because only 39 lambs observed during 2014 and 2015 were caught in August catches (equating approximately to weaning), and the majority of these lambs were born to females with high quality home ranges (only seven lambs born to females with *H. lanatus* covers lower than 30%), we used data spanning the period 1985 to 2015 for this analysis. Similarly, we used data spanning the period 1988 to 2015 to maximise the sample size for body condition analyses. In order to be consistent with the behavioural work we restricted our analyses to females aged between three and eight years old, that had given birth to singleton lambs. This left us with 1079 lambs (born to 533 females) for growth analyses and 1168 females for the body condition analyses. We calculated lamb growth as the change in weight (in grams) between birth in April/May and the catch in August divided by the number of days between birth and August weight measurements, and maternal body condition as the residuals from a linear regression of August body mass against hind leg length. There has been substantial debate over the accuracy of this measure of body condition (Green 2001; Schulte-Hostedde et al. 2005); however, due to data limitations we are unable to use more direct measures of condition. Both lamb growth and body condition were analysed using linear mixed effects models using lme4 (Bates et al. 2015). In both cases, maternal identity was

included as a random effect, with lamb year of birth included as a random effect in growth models, whilst the year of measurement was included as a random effect in models of maternal body condition. In lamb growth models, we included the lamb's sex, maternal age, and julian birth date as fixed effects, whereas in maternal body condition models we included only the female's age as a fixed effect. To test for an association between home range quality and both lamb growth and female body condition, we then compared these models with a model that also contained the percentage cover of *H. lanatus* in a female's annual home range as a fixed effect and another model containing a quadratic term for the mean annual home range percentage cover of *H. lanatus*. In both cases, we used home ranges calculated for the year preceding the lamb's birth. These models were also compared using AICc, with the best model taken to be that with the lowest AICc unless there was a more parsimonious model with a comparable AICc.

2.4 Results

2.4.1 Variation in home range quality

There was substantial between-individual variation in home range quality and habitat selection. Mean percentage covers of *H. lanatus* in female lifetime home ranges varied from 9.6% to 61.5%, with a similar pattern evident for annual home ranges, which had mean *H. lanatus* covers ranging from 10.2% to 64.3%. In the case of resource selection functions, there was considerable variation in the selection for the three broad community types (represented by the three principal components). The greatest variation was apparent in PC1 with beta coefficients for this principal component ranging from -12.8 to 1.0. In this case, the more negative the value, the greater the selection for plant species associated with grassland rather than species associated with heathland. The ranges for PC2 and PC3 were smaller than for PC1 but similar to each other at -0.1 to 9.6 and -0.8 to 9.9,

respectively. In the case of PC2, more positive values corresponded to greater selection for species associated with HA grassland relative to *Festuca-Plantago* swards, whilst for PC3, more positive values were associated with greater selection for areas rich in *Calluna vulgaris*.

2.4.2 Lamb behaviours

Likelihood ratio tests of models with and without the individual identity random effect indicated that there was between individual variation in suckling frequency with ($\chi^2(1) = 5.34$, p = 0.02) and without failed suckling events ($\chi^2(1) = 67.65$, p = < 0.0001), mean suckle duration (without failed suckling events - $\chi^2(1) = 14.07$, p = 0.0002), suckling success ($\chi^2(1) = 6.00$, p = 0.01) and grazing time ($\chi^2(1) = 5.45$, p = 0.02) even when fixed effects were accounted for. As expected, lamb age was a key predictor in models for all the lamb behaviours recorded over the period of maternal care, being present in the best fit model in all cases (Table 2.2). This suggests that our methods were effective in capturing variation in lamb behaviours over this period. All of the measures of sucking behaviour, as well as the total time a lamb spent resting, decreased as the lamb approached weaning (Table 2.2). However, these relationships were non-linear, with the reduction being most pronounced within the first weeks of life (Fig. 2.2). In contrast, the total time a lamb spent grazing during each observation increased as they approached weaning, though after around 70 days of age the total time a lamb spent grazing decreased slightly (Table 2.2).

We first used lifetime home range quality metrics in our analyses as the females in our study were selected based on this measure. We found no evidence for a significant association between any of the measures of sucking behaviour and the lifetime mean percentage cover of *H. lanatus* in a female's home range. Home range quality did not feature in the best fit model for any of the measures of lamb sucking behaviour (Table 2.2), and this result was consistent whether failed

suckling events were excluded or not (Appendix A Table S3). We also found no evidence for a significant relationship between a female's home range quality and any of the non-suckling behaviours recorded, with home range quality absent from the best fit models for both grazing time and resting time (Table 2.2).

When we used the annual home range quality metrics we also found that the mean percentage cover of *H. lanatus* was not important in explaining any of the lamb behaviours studied (Table 2.2). As for the analyses using lifetime home range quality metrics, the mean percentage cover of *H. lanatus* in a female's annual home range did not feature in the best fit models for suckling frequency, mean suckle duration, suckling success, total sucking time, total grazing time, or total resting time (Table 2.2). Furthermore, the results for the suckling behaviours were consistent whether failed suckling events were included or not (Appendix A Table S3). We also found that our results were equivalent when the absolute cover of *H. lanatus* in a female's home range was used, with this term absent from the best fit models for all lamb behaviours (Appendix A Table S2).

Analyses using resource selection function coefficients tended to produce similar results to analyses performed using home range quality metrics, with none of the three coefficients (PC1, PC2, or PC3) featuring in best fit models for suckling frequency, mean suckle duration, total grazing time or total resting time (Table 2.2). These results were also consistent when failed suckling events were excluded (Appendix A Table S3). In addition, when we performed models using resource selection coefficients that incorporated the error around the RSF parameter estimates our results were similar, with only 12 out of the 100 best fit models including any of the RSF coefficients. The one difference between the results of home range quality and RSF analyses came from models of suckling success. Suckling success was not explained by home range quality, whether lifetime or annual (Table 2.2). In contrast, when resource selection coefficients were used, both PC1 and PC3 featured in the best fit model for the proportion of successful

suckling events in first-order interactions with lamb age. These terms indicated that the relationship between suckling success and a female's habitat selection changed as the lambs aged (Table 2.2). When the lambs were young, there was little difference in suckling success with a female's selection for HA grassland; however, as the lambs approached weaning, individuals born to females exhibiting greater selection for heathland (communities dominated by *C. vulgaris*, *N. stricta* etc) had greater suckling success (Fig. 2.3). Similarly, as lambs aged, individuals born to females that selected for plant communities rich in *Calluna vulgaris* had greater suckling success (Table 2.2).

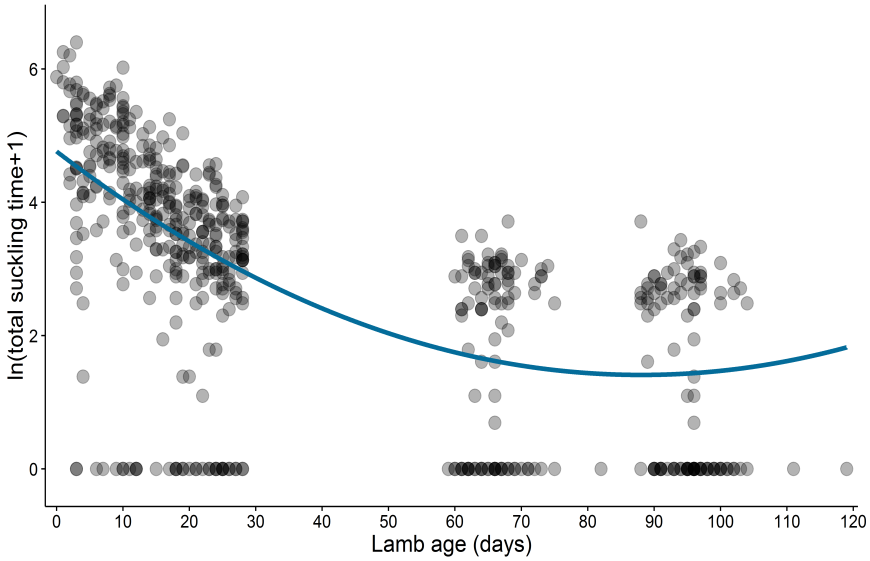

Figure 2.2: Total sucking time (log transformed) plotted against lamb age in days. The regression line comes from the full linear mixed model; however, to aid interpretation we plot the relationship for 2015 only.

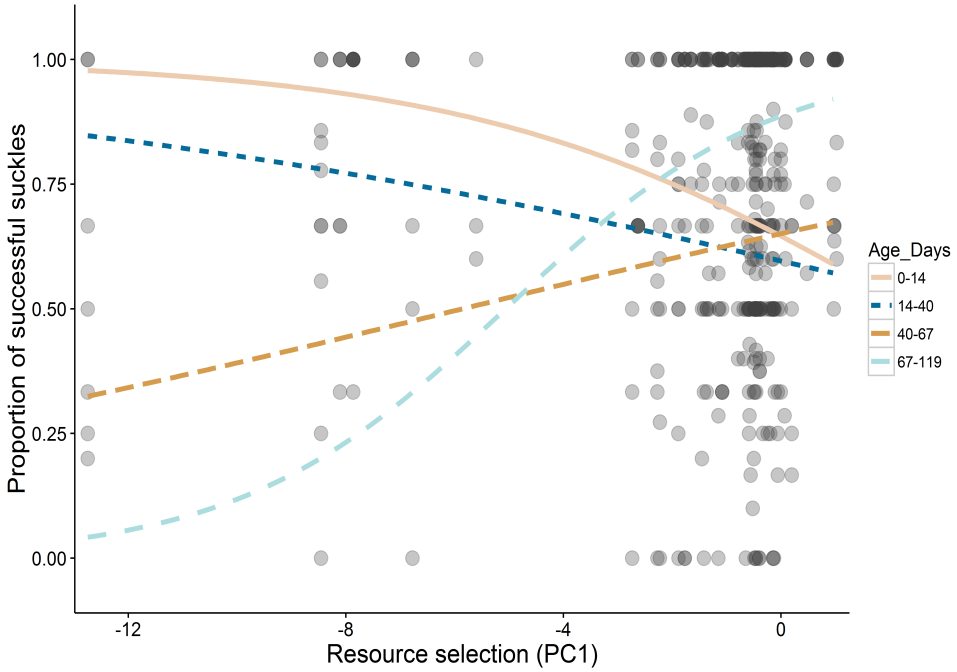

Figure 2.3: Plot illustrating the interaction between lamb age and PC1 in the best fit model for suckling success. The relationship between the proportion of successful suckling events in each observation (y axis) and individual PC1 coefficients (broadly describing the degree of selection for *Festuca-Plantago* swards) from resource selection functions vary depending on the age of the lamb, becoming more positive as the lamb ages. Each line represents the model prediction (from the full model) for a different set of lamb ages.

Table 2.2: Parameter estimates (± standard error) from the best fit models for all lamb behaviours (with and without failed suckling events), using lifetime home range quality estimates, annual home range quality estimates (A corresponds to the annual mean percentage cover of *H. lanatus*, whilst B corresponds to the annual absolute cover of *H. lanatus*) and annual resource selection function coefficients.

Trait	Term	Lifetime home range		Annual home range A		Annual home range B		Resource selection function	
		Est(SE)	t/z*	Est(SE)	t/z*	Est(SE)	t/z*	Est(SE)	t/z*
Suckling	Lamb age (days)	-1.09(0.06)	-19.76	-1.09(0.06)	-19.76	-1.09(0.06)	-19.76	-1.01(0.06)	-17.06
frequency	Year (2015)	0.34(0.10)	3.56	0.34(0.10)	$3.7\times e^{-4}$	0.34(0.10)	3.56	0.31(0.11)	2.83
	Maternal age	-0.04(0.03)	-1.25	-0.04(0.03)	-1.25	-0.04(0.03)	-1.25	-0.04(0.03)	-1.26
	Lamb age^2	0.35(0.06)	5.36	0.35(0.06)	5.36	0.35(0.06)	5.36	0.34(0.07)	5.20
Mean suckle	Lamb age (days)	-0.35(0.05)	-7.16	-0.35(0.05)	-7.16	-0.35(0.05)	-7.16	-0.35(0.05)	-7.16
duration	Year (2015)	-0.03(0.08)	-0.35	-0.03(0.08)	-0.35	-0.03(0.08)	-0.35	-0.03(0.08)	-0.35
	Maternal age	0.03(0.02)	1.11	0.03(0.02)	1.11	0.03(0.02)	1.11	0.03(0.02)	1.11
	Lamb age^2	0.26(0.06)	4.54	0.26(0.06)	4.54	0.26(0.06)	4.54	0.26(0.06)	4.54
Sucking time	Lamb age (days)	-1.41(0.08)	-17.75	-1.41(0.08)	-17.75	-1.41(0.08)	-17.75	-1.43(0.08)	-17.55
	Year (2015)	0.36(0.13)	2.76	0.36(0.13)	2.76	0.36(0.13)	2.76	0.38(0.13)	2.86
	Maternal age	$-6.6\times e^{-4}$(0.04)	-0.02	$-6.6\times e^{-4}$(0.04)	-0.02	$6.6\times e^{-4}$(0.04)	-0.02	0.003(0.04)	0.07
	Lamb age^2	0.49(0.09)	5.74	0.49(0.09)	5.74	0.49(0.09)	5.74	0.51(0.09)	5.81
Suckling	Lamb age (days)	-0.10(0.11)	-0.96	-0.10(0.11)	-0.96	-0.10(0.11)	-0.96	-0.005(0.12)	-0.04
success	Year (2015)	-0.17(0.17)	-1.04	-0.17(0.17)	-1.04	-0.17(0.17)	-1.04	-0.11(0.17)	-0.67
	Maternal age	0.08(0.04)	1.74	0.08(0.04)	1.74	0.08(0.04)	1.74	0.09(0.05)	1.93
	Lamb age^2	0.39(0.13)	2.98	0.39(0.13)	2.98	0.39(0.13)	2.98	0.49(0.13)	3.63
	PC1	-	-	-	-	-	-	0.002(0.06)	0.04
	PC3	-	-	-	-	-	-	-0.06(0.10)	-0.61
	Lamb age:PC1	-	-	-	-	-	-	0.24(0.06)	3.79
	Lamb age:PC3	-	-	-	-	-	-	0.26(0.09)	2.80
Grazing time	Lamb age (days)	2.86(0.13)	21.84	2.86(0.12)	21.84	2.86(0.13)	21.84	2.86(0.13)	21.84
	Year (2015)	-0.04(0.23)	-0.19	-0.04(0.23)	-0.19	-0.04(0.23)	-0.19	-0.04(0.22)	-0.19

	Maternal age	-0.004(0.07)	-0.06	-0.004(0.07)	-0.06	-0.004(0.07)	-0.06	-0.004(0.07)	-0.06
	Lamb age^2	-1.66(0.14)	-11.79	-1.66(0.14)	-11.79	-1.66(0.14)	-11.79	-1.66(0.14)	-11.79
Resting time	Lamb age (days)	-332.29(57.97)	-5.73	-332.29(57.97)	-5.73	-332.29(57.97)	-5.73	-332.29(57.97)	-5.73
	Year (2015)	-80.95(88.02)	-0.92	-80.95(88.02)	-0.92	-80.95(88.02)	-0.92	-80.95(88.02)	-0.92
	Maternal age	12.10(27.61)	0.44	12.10(27.61)	0.44	12.10(27.61)	0.44	12.10(27.61)	0.44
	Lamb age^2	150.88(62.51)	2.41	150.88(62.51)	2.41	150.88(62.51)	2.41	150.88(62.51)	2.41

* t values are reported for linear mixed effects models whilst z values are reported for generalised linear mixed effects models.

2.4.3 Female behaviours

We also found that female behaviours varied with lamb age, with grazing frequency declining with lamb age and both resting frequency and moving frequency increasing with lamb age (Table 2.3). As for lamb behaviours, there was no evidence for consistent variation in female behaviour with home range quality. The mean percentage cover of *H. lanatus* in a female's lifetime home range did not feature in the best fit model for grazing frequency, moving frequency or resting frequency (Table 2.3). The same was generally true when we used annual home range quality metrics. Both the annual mean percentage cover of *H. lanatus* and annual absolute cover of *H. lanatus* were absent from the best fit models for all the female behaviours studied, except in the case of movement frequency when the number of overlapping females was included (Table 2.3 and Appendix A Table S2). When the density term was included the absolute cover of *H. lanatus* featured in the best fit model, suggesting that females with higher quality home ranges spent more time moving per hour of observation (Appendix A Table S2). Our results were also largely comparable when we used coefficients from individual resource selection functions in place of home range quality metrics, with none of the three principal components featuring in the best fit models for grazing frequency or resting frequency (Table 2.3). The results for moving frequency did differ slightly when using the resource selection coefficients, with PC2 featuring in the best fit model in a first order interaction with lamb age (Table 2.3). This term indicated that females who selected more highly for *Festuca-Plantago* swards spent more time moving.

Table 2.3: Parameter estimates (± standard error) from best models for all female behaviours, using lifetime home range quality estimates, annual home range quality estimates (A corresponds to the annual mean percentage cover of *H. lanatus*, whilst B corresponds to the annual absolute cover of *H. lanatus*) and annual resource selection function coefficients.

Trait	Term	Lifetime home range		Annual home range A		Annual home range B		Resource selection function	
		Est(SE)	z	Est(SE)	z	Est(SE)	z	Est(SE)	z
Grazing frequency	Lamb age (days)	-0.14(0.02)	-7.96	-0.14(0.02)	-7.96	-0.14(0.02)	-7.96	-0.14(0.02)	-7.96
	Year (2015)	0.06(0.03)	1.74	0.06(0.03)	1.74	0.06(0.03)	1.74	0.06(0.03)	1.74
	Maternal age	0.005(0.01)	0.48	0.005(0.01)	0.48	0.005(0.01)	0.48	0.005(0.01)	0.48
Resting frequency	Lamb age (days)	0.48(0.08)	5.79	0.48(0.08)	5.79	0.48(0.08)	5.79	0.48(0.08)	5.79
	Year (2015)	-0.43(0.17)	-2.57	-0.43(0.17)	-2.57	-0.43(0.17)	-2.57	-0.43(0.17)	-2.57
	Maternal age	-0.009(0.05)	-0.17	-0.009(0.05)	-0.17	-0.009(0.05)	-0.17	-0.009(0.05)	-0.17
Moving frequency	Lamb age (days)	0.11(0.06)	1.73	0.11(0.06)	1.73	0.11(0.06)	1.73	0.20(0.09)	2.34
	Year (2015)	0.43(0.17)	2.48	0.43(0.17)	2.48	0.43(0.17)	2.48	0.47(0.17)	2.68
	Maternal age	-0.02(0.05)	-0.47	-0.02(0.05)	-0.47	-0.02(0.05)	-0.47	-0.04(0.05)	-0.84
	PC2	-	-	-	-	-	-	-0.10(0.06)	-1.65
	Lamb age:PC2	-	-	-	-	-	-	0.08(0.05)	-1.59

Table 2.4: Parameter estimates (± standard error) for full and best models of lamb growth (between birth and weaning) and maternal body condition. In both cases home range qualities were derived from annual home ranges.

	Term	Full model		Best model	
		Est (SE)	t	Est (SE)	t
Lamb growth	Maternal age	0.13(0.26)	0.48	0.12(0.26)	0.48
	Sex (male)	14.43(0.80)	18.02	14.43(0.80)	18.02
	Birth date	0.57(0.09)	6.41	0.57(0.09)	6.50
	HR quality	-0.06(0.22)	-0.26	-	-
	HR quality^2	$7.8\times e^{-4}$(0.003)	0.27	-	-
Maternal body condition	Maternal age	0.20(0.03)	7.36	0.20(0.03)	7.32
	HR quality	-0.03(0.07)	-0.41	-	-
	HR quality^2	-0.10(0.06)	-1.62	-	-

2.4.4 Lamb growth and maternal body condition

Lamb growth between birth and August varied with both birth date and sex, with late born lambs and male lambs growing more quickly over this period (Table 2.4). However, there was no indication that lamb growth varied in relation to the quality of their mother's home range in the year preceding their births as this term was not included in the best fit model (Table 2.4). There was also no indication that the quality of a female's home range in the year preceding the birth of her lamb affected her body condition in the following August (Appendix A Fig. S3). The AICc of the model including home range quality (both linear and quadratic term) was equivalent (<2 unit difference) to the best model (selected following rules of parsimony); however, it was apparent from this model that the relationship between home range quality and female body condition was very weak (Appendix A Fig. S3).

2.5 Discussion

In this study, we examine the role of individual-level, as opposed to population-level, variation in resource availability on post-natal maternal care in a wild-living mammal. We found no evidence that variation in female or lamb behaviour over the period of maternal care was associated with variation in the quality of the home range occupied by a female Soay sheep. There was no indication that suckling frequency, or the mean duration of suckles varied with home range quality, and consequently there was no significant relationship between the quality of a female's home range and the total time her lamb spent sucking. There was also no indication that the quality of a female's home range influenced her lamb's grazing and resting behaviour. Similarly, we found no association between either lifetime or annual home range quality and female grazing, resting or movement frequency. Our behavioural results were supported by our analyses of

lamb growth, where we found that the quality of a female's home range had no influence on the weight gain of her lambs between birth and weaning. This also suggests that lambs born to females with home ranges of differing qualities did not receive differing levels of investment. In addition to providing comparable levels of care, females were in similar condition in the August following the birth of their lamb despite having home ranges of differing qualities. This may explain why a previous analysis found no apparent relationship between home range quality and female lifespan (Regan et al. 2016).

Though it is somewhat surprising that Soay sheep females do not adjust their investment into maternal care given the quality of their home range, we feel our results are robust for the following reasons. First, our sample size of 69 individuals is large relative to that of many similar studies using wild populations (e.g. Tremblay et al. 2004 - 26 individuals, Robertson et al. 1992 - 44 females with singletons, and Andersen et al. 2000 - 24 individuals). Second, by observing each female and her lamb over the entire period of maternal care, our results were not biased by examining the relationship between resource availability and care over a shorter time scale. Third, we recorded non-suckling behaviours both of the female and the lamb, making it possible to examine whether the female or lamb adjusted such behaviours in response to the pattern of care. Finally, although the characterization of the resources available to an individual is complex, our results were robust across different measure of resource use, suggesting that resource variation was accurately captured. When using coefficients from RSFs, we found an association between female movement frequency and resource use that was not apparent in analyses using *H. lanatus* cover. This result suggests that females who select for *Festuca-Plantago* dominated swards moved more frequently during observations. It is not particularly surprising that we did not detect this trend with models using only *H. lanatus* covers as the amount of HA grassland in a female's home range is unlikely to correlate strongly with the amount of *Festuca-Plantago*

sward within their home range, particularly as *Festuca-Plantago* swards are relatively restricted to the west of the study area. Individuals in these areas are also the least accustomed to human activity and as a result, are the most sensitive to human disturbance. It is therefore possible that this result is due to increased movements made by these individuals as a result of tourist disturbance.

Variation in resource availability is expected to alter the amount of parental care through its effects on the relative costs and benefits of parental care (Clutton-Brock et al. 1991). Despite this, it has often proved difficult to demonstrate a link between resource availability and parental care behaviour, as illustrated by our work and numerous other studies (e.g. Whittingham and Robertson 1994, Andrews et al. 2016). It seems unlikely that variation in resource availability would not affect the costs and benefits of parental care, but it is possible that this effect does not translate into the predicted difference in parental care behaviour. In our case we can exclude any effects due to the behaviour of a partner as only females provide care in this species. It is possible that behavioural measures of parental care may not accurately reflect the transfer of resources from parent to offspring. For instance, in the case of mammals, there is criticism surrounding the use of suckling behaviour as an indicator of milk intake (summarised in Cameron (1998)) and maternal investment during lactation. For example, mothers may vary in the nutritional content of their milk, and offspring may therefore receive very different amounts of nutrition for the same amount of time spent sucking (Skibiel and Hood 2015). Furthermore, individual offspring may differ in the efficiency with which they obtain milk (Cameron 1998). Despite these concerns, we believe that our approach has characterised variation in parental care in Soay sheep. First, by observing individuals at various times throughout the day and across the entire maternal care period, it is unlikely that our results are biased due to within-day or seasonal variation in suckling behaviour. Second, by measuring non-suckling behaviours of both a female and her lamb, we obtained a more complete picture of

each individual's decisions over this period. For example, by recording grazing behaviour we were able to look for evidence of compensation by the female or her lamb for the level of parental care. Finally, because of the long-term nature of the St. Kilda Soay sheep project, we had access to a larger sample of growth data to validate any results from our behavioural observations. The results of this analysis confirm that variation in home range quality does not influence post-natal maternal care. This period includes a significant portion of time over which the lamb is able to supplement the nutrition gained from its mother by grazing, which may complicate any analysis of the relationship between home range quality and maternal care. Nevertheless, our results show that lamb grazing behaviour does not vary with home range quality, supporting our suggestion that females with home ranges that differ in quality invest similarly into maternal care.

Our finding that environmental conditions have no effect on parental care has implications for our understanding of reproductive strategies in ungulates. Previous studies suggest that female ungulates tend to favour their own survival and reproduction over that of their offspring under poor conditions, thereby exhibiting a conservative reproduction strategy. For example, studies on bighorn sheep (*Ovis canadensis*) and white-tailed deer (*Odocoileus virginianus*) suggest that females exhibit bet-hedging strategies, such that there is little change in female mass/survival but there are significant reductions in offspring mass/survival when conditions are poor (Festa-Bianchet and Jorgenson 1998; Therrien et al. 2007; Martin and Festa-Bianchet 2010). In addition, other studies show that variation in forage quality between years or between populations is associated with behavioural differences or variation in offspring growth. For example, mountain goat (*Oreamnos americanus*) kids in Alberta, Canada, grow faster in years where forage quality is high (Côté and Festa-Bianchet 2001a). Similarly, a recent study on Appennine chamois (*Rupicapra pyrenaica ornata*) found reductions in maternal care when pasture quality was poor (Scornavacca et al. 2016). Long-lived

iteroparous species such as ungulates are expected to follow a conservative reproduction strategy, given that parents should favor their own reproduction when resource scarcity has a smaller impact on the future reproduction of the parent compared to that of the offspring (Clutton-Brock et al. 1991). For this reason, we would also expect female Soay sheep to show such a pattern because their fitness is determined to a greater degree by their own survival and reproduction than that of offspring from any single litter (Clutton-Brock et al. 1996). However, in contrast to the above studies, we found no evidence that reduced home range quality altered the level of maternal care or the mass gain of lambs. Therefore, there was little evidence to suggest that female Soay sheep exhibit a conservative reproductive strategy in response to spatial variation in resource availability.

One of the key reasons for why we did not find evidence for a conservative reproductive strategy in this study may lie in the specific biology of the St. Kilda Soay sheep. This population is characterised by instability, with periodic population crashes in which up to 70% of the animals on the island die (Clutton-Brock et al. 2004). Previous research suggests that Soay sheep females do not base decisions about reproductive investment upon information about future trends in population density, instead using information on current nutrition, body mass, and age (Marrow et al. 1996). Potentially, all females in our study were able to meet the costs of lactation regardless of the area in which their home range was located. Given that they were likely to be of high quality as heavier females are more likely to survive winter (Clutton-Brock et al. 1996), and that competition for vegetation during the summer is low due to the high productivity during this period (Crawley et al. 2004), all of our study females may have been able to counteract the costs of providing a high level of maternal care by consuming high quality resources during the high productivity period. Indeed, some studies using other systems have suggested that increased nutrient intake may be a cause for the absence of costs of reproduction (e.g. Hamel et al. 2009). The ability of the females to compensate for

the costs experienced due to providing maternal care might explain why we did not detect any variation in lamb weight gain between birth and August given variation in female home range quality/resource selection, and why a previous study found no indication that lamb survival to weaning varied with the mean percentage cover of *H. lanatus* in a female's lifetime home range (Regan et al. 2016). Similarly, it may explain why lambs born to mothers with home ranges of higher quality have greater suckling success early in the season when vegetation is still limiting, whilst the opposite is true later in the summer when resource availability is high. This may indicate that females that differ in their use of space exhibit slightly different patterns of care over this period despite provisioning similarly over the total maternal care period. However, this result was driven partially by a lack of data for individuals with very negative PC1 and positive PC3 coefficients. Therefore to validate this interpretation, it would be necessary to study females that were more evenly distributed across the continuum of PC1 and PC3 values.

In both 2014 and 2015, twinning rates were low and we were therefore unable to include any twin litters in our sample. The reproductive costs of having a twins is likely to be greater than the costs resulting from having a singleton. As a result, the benefit of having a high quality home range may be more pronounced for females with twins. This is particularly pertinent given that, in many of the ungulate populations where conservative reproductive strategies have been illustrated, twinning does not occur or is very rare [e.g. mountain goat (Côté and Festa-Bianchet 2001a), bighorn sheep (Gaillard et al. 2000), chamois (Serrano et al. 2015)]. These studies may have been better capturing the behaviour of individuals experiencing the greatest costs as a result of providing care. However, we feel that the lack of twins in our study is unlikely to be responsible for our results given that only the heaviest females give birth to twins (Clutton-Brock et al. 2004) and these individuals are likely to be able to better cope with the costs of providing care. Such a relationship may mean that an association between habitat use and

maternal care provisioning would still be absent even if twin litters were included. Given the marked fluctuations in population density on St. Kilda, the conditions in the year when observations are conducted are likely to be important in determining the behavioural patterns observed. Indeed, the study by Robertson et al. (1992) showed that suckling behaviour varies between years in St. Kilda Soay sheep. If we had conducted our observations in years where density in the previous winter had been low, the majority of individuals would have been in good condition in Spring, such that there would be little variation in the care they provide. This was not however the case, with high population density in the summer preceding both years of observation, at 545 individuals in the study area in the August of 2013 and 482 in the August of 2014. This is in contrast to recent lows of 362 and 335 in 2012 and 2002. We must consider the fact that variation in local density across the study area might have precluded an association between maternal care and home range quality, as higher density in areas of high quality might result in these areas being devalued. However, sheep consistently favour *Holcus-Agrostis* grassland, even when densities are high, potentially as a result of this community being more resilient to grazing pressure than other community types including wet and dry heath (Jones et al. 2005). Therefore, our result is unlikely to be entirely driven by variation in local density.

Our work adds to the existing literature on the effects of resource availability on parental care by examining the effect of spatial variation in resource availability quantified at the individual scale. In contrast, many of the previous studies have used resource availability estimates at the study area scale to study the effect of temporal variation in resources (e.g. Rachlow and Bowyer 1994 and Andersen et al. 2000), or have examined the effect of spatial variation in resource availability by estimating resource quantity/quality at scales above that of the individual home range (e.g. regions differing in the availability of nutritious pasture [Scornavacca et al. 2016]). Individuals are more likely to respond to the resource availability they

experience in their home range than to the resources available in the study area or the area in which the population persists because it is the resource availability at this scale that will determine the costs and benefits of care. Furthermore, different parts of a study area may vary in how the quantity/quality of resources varies over time, or indeed in more subtle fine-scale spatial patterns in resource availability. It is also likely that an individual's response to temporal variation in the environment, for example variation in density and weather conditions between years may be conditional on the environmental conditions it experiences on a within-year basis. We therefore feel that there is a need to conduct further studies based on the approach used in our study, which quantify resource availability at the individual scale in order to understand how environmental conditions influence the behaviour of individuals. Movement ecology has provided the tools to quantify resource availability at the individual scale, and though the necessary data can be hard to come by we hope that the advance in tracking technologies, combined with reductions in the cost of using these technologies will make more studies of this kind possible.

In conclusion, we find that female Soay sheep vary substantially in their home range quality and in their selection for different plant communities, but there is nevertheless no evidence that home range quality influences their investment into maternal care, as indicated by both suckling behaviour and estimates of lamb growth over the summer. There was no evidence that either the female or her lamb adjusted any of the non-suckling behaviours measured (such as grazing or resting). This suggests that females inhabiting areas of Village Bay with poorer vegetation did not compensate for the level of care they provided by for example spending a greater amount of their time grazing. Our study suggests that female Soay sheep with poorer quality home ranges do not maintain their own survival and reproduction at a cost to the survival of their lambs. We suggest that this is because females giving birth to a lamb in spring, particularly following high

densities in the preceding winter, are in relatively good condition, and that resources are not limiting during the summer. This may mean that no matter where a female's home range is located, she is able to offset the costs of lactation by consuming additional resources. Our results demonstrate the need to examine the effect of resource variation quantified at the individual scale on individual reproductive investment decisions. Combining this approach with studies examining the effect of temporal variation in the environment on reproductive investment decisions may provide us with a more complete picture of the influence of resource availability on reproductive investment in natural populations.

Chapter 3

Costs of reproduction in female Soay sheep are not influenced by variation in access to a high quality plant community

3.1 Abstract

The cost of reproduction is arguably the most studied life-history trade-off, occurring when investment into a reproductive attempt results in reduced future survival and/or reproduction. Absence of the cost of reproduction may be explained by environmental or individual heterogeneity because they affect the resources available to individuals. Despite this, there has, to our knowledge, been little research to understand how between-individual differences in resource acquisition, caused by variation in phenotype and, in particular, space use, interact with environmental variation occurring at the population scale to determine the cost of reproduction experienced by individuals in natural populations. We used long-term data from the St. Kilda Soay sheep population to understand how differences in age, home range quality, and average adult body mass, interacted with annual variation in population density and winter North Atlantic Oscillation index to influence over-winter survival, and the probability of reproduction and twinning in the subsequent year, for females that had invested into reproduction to varying degrees. Our results suggest that Soay sheep females experience substantial survival costs, and that old individuals breeding in high density years experience costs in terms of future reproduction, but that these costs do not vary given an individual's home range quality. There was no apparent cost in terms of a female's twinning probability, but it was evident that females with high quality home ranges were more likely to bear twins. There are a number of possible causes for the lack of a relationship between home range quality and the costs experienced by female Soay sheep. These include the fact that resources may not be limiting during the summer when females are investing the most energy into reproduction, and the possibility that our measure of home range quality is not estimated at the most appropriate temporal or spatial scale.

3.2 Introduction

Organisms are continually faced with choices over how to use the limited resources available to them, with individuals being expected to partition these resources for investment in growth, reproduction, and survival such that their fitness is maximised (Williams 1966; Stearns 1989). This is expected to give rise to trade-offs, where a beneficial change in one trait results in a detrimental change in another (Stearns 1989). For example, the increased allocation of resources to a reproductive event is expected to result in reduced survival and/or future reproduction, a trade-off that is referred to as the 'cost of reproduction' (Bell 1980). The cost of reproduction has been the focus of extensive study for many years due to its potential role in shaping population dynamics (Hutchings 1999; Jacquemyn et al. 2010) as well as their possible consequences for the evolution of reproductive tactics (Bell 1980). Such work has illustrated a significant cost of reproduction for a wide range of taxa, both vertebrates (Nager et al. 2001; Tavecchia et al. 2001; Koivula et al. 2003; Moyes et al. 2006) and invertebrates (Kotiaho and Simmons 2003; Creighton et al. 2009; Papadopoulos et al. 2010). However, negative correlations between current reproduction and future survival and/or reproduction are not always found (Pettifor et al. 1988; Hare and Murie 1992). In fact, positive correlations between current reproductive investment and future performance have been discovered in a variety of species, including deer mice (*Peromyscus maniculatus*) (Millar et al. 1992) and willow tits (*Poecile montanus*) (Orell et al. 1996).

The lack of consistent evidence for a cost of reproduction may be explained by both environmental heterogeneity and differences in individual characteristics because they are likely to determine the resources available to individuals to invest into life-history traits. If resources are plentiful, individuals may be able to compensate for the cost of reproduction by consuming more resources (Bonnet

et al. 2002; Ruckstuhl and Festa-Bianchet 2010), whilst this cost may be more pronounced when conditions are particularly harsh, for example at high density (Clutton-Brock et al. 1996; Festa-Bianchet et al. 1998), when winter conditions are poor (Barbraud and Weimerskirch 2005; Tavecchia et al. 2005), or during disease outbreaks (Descamps et al. 2009b; Garnier et al. 2016). Similarly, between-individual differences in resource acquisition might explain the absence of the cost of reproduction or may even lead to the counter-intuitive positive correlations between reproductive investment and survival and/or future reproduction, something that was first proposed by van Noordwijk and de Jong (1986). They suggested that individuals that acquire more resources would likely be able to invest more into a current reproductive event without incurring more costs than individuals that acquire fewer resources. Such differences between individuals could arise in multiple ways, such as through age (Tavecchia et al. 2001; Descamps et al. 2009a) and body mass (Festa-Bianchet et al. 1998) or condition (Cichoń et al. 2008), and the incorporation of measures of individual heterogeneity can help to reveal significant costs in some, but not all situations (Hamel et al. 2010b).

Despite this interest in the effect of variation in resource acquisition on the cost of reproduction experienced by individuals, there has, to our knowledge, been little attempt to understand how between-individual differences in resource acquisition due to differences in phenotype and individual variation in space use interact with large scale environmental variation (e.g. population density and weather) to determine the cost of reproduction experienced by individuals in natural populations. A study of this kind requires a combination of detailed long-term environmental data and extensive longitudinal data on individual animals, including data on individual variation in resource use. Such data are available from the long-term individual based study of the St. Kilda Soay sheep, making this population ideal for such a study. Not only are individuals within this population followed from birth until death, providing detailed information on survival,

reproduction, and space use, there is a wealth of data for a wide variety of environmental components, such as population density, local weather, and access to resources (i.e. plant community composition within an individual's home range). Previous research has established that female Soay sheep experience substantial survival costs as a result of reproduction, particularly in years of high density and severe weather, but there is no evidence for costs expressed as a reduction in future fecundity (Clutton-Brock et al. 1996; Tavecchia et al. 2005). In this work, we aimed to understand how differences in individual resource acquisition, due to phenotypic differences and variation in access to resources (home range quality), interacted with annual variation in population density and weather conditions to influence the fitness costs associated with reproduction experienced by female Soay sheep.

3.3 Methods

3.3.1 Study population

The feral Soay sheep population on the island of Hirta in the St. Kilda archipelago, Scotland, have been studied in detail since 1985 (Clutton-Brock et al. 2004). This long-term study centres on the one third of the island population that resides in Village Bay area. Individuals are marked with ear tags at birth and are subsequently followed throughout their lives, and there is detailed information on individual reproduction and survival for more than 10,000 individuals. Although the majority of prime-aged females reproduce each year, individual body mass influences both the likelihood that individuals will reproduce in their first year of life and the probability of twinning later in life (Clutton-Brock et al. 2004). Female Soay sheep experience survival costs of reproduction, with such costs appearing to vary with factors such as density, weather, and age (Clutton-Brock et al. 1996; Tavecchia et al. 2005). Despite this evidence that reproduction influences subsequent survival, there is no evidence to suggest that a female's reproductive

investment influences her future fecundity (Clutton-Brock et al. 1996).

3.3.2 Survival and reproduction data

This study uses data for all females born in/after 1985 and that survived to at least one year of age (the earliest point at which a female can reproduce) as determined by their date of death or census observations, and that were known or believed to be dead by the end of 2015. For each year of an individual's life, we classified its reproductive status in two ways. First, we assigned individuals as having bred or not bred (as in previous studies e.g. Tavecchia et al. (2005)), based on whether they were seen with a lamb during the lambing season or were confirmed to have had a lamb using genetic data. Second, we classified individuals as having not bred, having given birth to a singleton or twins that they did not wean, having given birth to a singleton that they successfully weaned, or having given birth to twins of which they weaned at least one (given that twinning rates are relatively low in this population, we did not have sufficient data to divide twinning females that weaned one lamb and those that weaned both). Successful weaning was classified as survival of the lamb until August of their year of birth (when they are around four months old) using data on the lamb's year of death, capture data, or census observations.

To examine survival costs of reproduction, we determined whether females survived until May the year after a potential reproductive bout as a measure of survival over the winter when mortality is greatest (Clutton-Brock et al. 2004). We did this using either dates of death, information on subsequent reproduction, or census data confirming that an individual was alive in a subsequent census. In cases where an individual's survival could not be conclusively determined because it had not been assigned a month of death and had no subsequent reproductive or census data, we classified them as having died because the absence of a month of death likely means that they died over-winter before the spring expedition to the

island, at which point it can be difficult for a month of death to be assigned. Furthermore, if females died shortly after giving birth in the subsequent April, they were recorded as having survived. To study costs in terms of future reproduction, we used lambing observations and genetically assigned maternities to classify whether females had reproduced in each year of their life. We also determined whether females had given birth to a singleton or twins to understand whether females that had invested more into reproduction experienced greater costs in terms of reduced twinning probability in the subsequent year.

3.3.3 Environmental data and individual resource acquisition

To examine the effect of between-year environmental variation on the costs of reproduction experienced by female Soay sheep, we characterised population density and winter weather. To capture variation in population density, we used the number of adults (> two years old) in the Village Bay study area recorded in the August census in the year of the reproductive episode. To characterise variation in the severity of winter weather, we used the North Atlantic Oscillation index (NAO), which has been shown to capture the effect of winter weather on ungulate survival and reproduction (Coulson et al. (2001); Catchpole et al. (2004); Pioz et al. (2008), but see Kjellander et al. (2006); Martínez-Jauregui et al. (2009)). The NAO is calculated as the difference between the normalised sea-level pressure at weather stations in Ponta Delgada (Portugal) and Reykjavik (Iceland), and winter NAO (average over December-March) provides a measure of winter weather in western Europe (Hurrell 1995). High NAO values correspond to mild, wet and stormy winters which are associated with reduced over-winter survival (Coulson et al. 2001). We obtained NAO values for the period of 1985-2016 from https://crudata.uea.ac.uk/cru/data/nao and averaged values from December to March of each year to obtain a measure of weather severity in the winter following each reproductive episode.

We also included two variables to capture variation in individual resource acquisition. The first was an individual's average adult body mass in kilograms, which may capture phenotypic differences between individuals that influence the amount of resources that are available for reproduction. We selected body mass because it is known to be a key determinant of female reproduction and survival in this population (Clutton-Brock et al. 2004). We calculated individual average body mass as the mean of August body mass measurements between the ages of two and six. We specifically used body mass measurements between two and six years old to capture the average body mass of individuals during prime age and to exclude as few animals as possible, given that not all individuals are captured each August.

The second variable used to describe individual resource acquisition was annual home range quality. The Village Bay study area consists of a variety of plant communities, including heaths such as *Calluna* wet heath, wet grasslands such as *Sphagnum* grassland and high quality grasslands such as *Holcus-Poa* and *Holcus-Agrostis* grasslands (Gwynne et al. 1974). The most productive of these communities is *Holcus-Agrostis* grassland, which is highly palatable to the sheep and preferred even at high density (Jones 2003). *Holcus lanatus* is a key constituent of this community and higher mean percentage covers of this plant within individual home ranges have been shown to be associated with higher female lifetime reproductive success (Regan et al. 2016). We therefore characterised an individual's home range quality in each year of life as the mean percentage cover of *Holcus lanatus*. Home ranges were estimated using census observations from the three census periods in each year (April/May, July/August, and October/November) using kernel density estimation methods in 'adehabitatHR' (Calenge 2006) in R version 3.1.3 (R Development Core Team 2008). We restricted our analyses to cases where individuals had been observed at least 16 times during the year because incremental area analysis indicated that this is the number of observations needed to get an asymptote in core home range area (70% isopleth).

Although individuals can have up to 30 census observations each year, this approach did result in the exclusion of individuals in some years, as only 404 (of 870) females had the necessary number of observations for every year of their life. To prevent individuals from having multiple observations with the same coordinates (which can make home range estimation problematic Tufto et al. (1996)), we added a random number between -20 and 20 (representing 20 metres) to X and Y coordinates of each observation. When estimating home ranges, we used the reference bandwidth (h_{ref}) rather than the *ad hoc* bandwidth recommended by Kie (2013) because we have previously found that both methods produce comparable home range quality estimates (Regan et al. 2017b). Between 2008 and 2012, 160 hectares of Village Bay were surveyed and all vascular plants present in each hectare were identified. At the same time, the percentage cover of each species (to the nearest 5%) was scored by eye. For each annual home range, we identified the hectares contained within the 70% isopleth and calculated the mean *H. lanatus* cover across the constituent hectares. We used the proportion of the hectare contained within the home range as a weight to ensure that hectares covering a greater proportion of the home range also contributed more to the home range quality measure.

3.3.4 Female survival and reproduction analyses

If females successfully reproduced in a given year, we tested for effects on the probability of over-winter survival, reproduction in the subsequent year, and twinning using generalised linear mixed models in the package lme4 (Bates et al. 2015) in R version 3.1.3 (R Development Core Team 2008). In each case, the response variable was binary and we therefore assumed a binomial distribution and used a logit link in each case. To aid convergence, we used the 'bobyqa' optimiser and increased the number of iterations to one million. All models included female age (in years) as a fixed effect. In the case of over-winter survival, we used female

age when reproductive status (whether investment into lactation was taken into account or not) was determined whilst we used female age in the year following the assignment of reproductive status when analysing future reproduction and twinning probability. Survival models included the year of reproduction (the year in which an individual's reproductive status was assigned) as a random effect, whilst future reproduction and twinning models included both female ID and the reproductive year as random effects.

To understand how a female's investment into reproduction affected her survival, reproduction, and twinning probability in the subsequent year, we used a series of models, detailed in Table 3.1. The fixed effects included in these models were female age (linear and quadratic terms were), a female's average adult body mass, home range quality in the previous year, population density in the previous August, the NAO in the previous winter, and a female's reproductive status. As mentioned above, each female had two reproductive status values, depending on whether investment into lactation was taken into account. Therefore, reproductive status was incorporated as either a two level (bred or did not breed) or four level factor (did not breed, did not wean, weaned singleton, or weaned twin(s)).

Models 1 to 3 allowed us to understand how simply accounting for variation in individual resource acquisition and between-year variation in environmental conditions influenced the estimates of the effect of reproductive status. Models 4 to 8 allowed us to understand whether there was any evidence that the effect of reproductive status was influenced by individual differences or annual variation in the environment, and Models 9 to 15 enabled us to further understand whether any variation in the costs of reproduction given between-year variation in density and winter weather was influenced by differences in resource acquisition. We used Akaike's Information Criterion corrected for small sample size (AICc) to compare these models and the model with the lowest AICc determined as the best model in each case.

3.3.5 Models without resource acquisition

The use of average adult mass and annual home range quality to describe variation in individual resource acquisition resulted in the exclusion of some individuals. This exclusion tended to be biased towards short-lived females, particularly those that died after their first potential reproductive attempt. Because reproductive costs may be pronounced in young individuals (Tavecchia et al. 2005; Descamps et al. 2009a), we repeated our analyses without these variables to better understand the influence of age on the costs experienced by females in this population. To do this, we compared a smaller set of models Table 3.2 to investigate whether survival, reproduction, and twinning varied with reproductive status when accounting for variation in density and winter weather between years, and to test whether there was any evidence that the effect of reproductive investment varied given individual age and ecological conditions. Again, the best model was the one with the lowest AICc.

Table 3.1: Models used in the analyses of survival, reproduction, and twinning probability when average adult body mass and annual home range quality were included.

Model	Fixed effects	Random effects
1	Reproductive status + age + age^2	Year† + maternal ID‡
2	Reproductive status + age + age^2 + body mass + home range quality	Year† + maternal ID†
3	Reproductive status + age + age^2 + body mass + home range quality + density + NAO	Year† + maternal ID‡
4	Reproductive status*age + reproductive status*age^2 + body mass + home range quality + density + NAO	Year† + maternal ID‡
5	Reproductive status*body mass + age + age^2 + home range quality + density + NAO	Year† + maternal ID‡
6	Reproductive status*home range quality + age + age^2 + body mass + density + NAO	Year† + maternal ID‡
7	Reproductive status*density + age + age^2 + body mass + home range quality + NAO	Year† + maternal ID‡
8	Reproductive status*NAO + age + age^2 + body mass + home range quality + density	Year† + maternal ID‡
9	Reproductive status*age*density + reproductive status*age^2*density + body mass + home range quality + NAO	Year† + maternal ID‡
10	Reproductive status*age*NAO + reproductive status*age^2*NAO + body mass + home range quality + density	Year† + maternal ID‡
11	Reproductive status*body mass*density + age + age^2 + home range quality + NAO	Year† + maternal ID‡
12	Reproductive status*body mass*NAO + age + age^2 + home range quality + density	Year† + maternal ID‡
13	Reproductive status*home range quality*density + age + age^2 + body mass + NAO	Year† + maternal ID‡
14	Reproductive status*home range quality*NAO+ age + age^2 + body mass + density	Year† + maternal ID‡
15	Reproductive status*density*NAO+ age + age^2 + body mass + home range quality	Year† + maternal ID‡

† Year corresponds to the year when reproductive status was assigned when modelling over-winter survival, and the year of the reproductive event being modelled in the case of reproduction and twinning probability.

‡ Maternal ID only included in models of reproduction and twinning probability.

Table 3.2: Models used to analyse survival, reproduction, and twinning probability when average adult body mass and annual home range quality were excluded in order to include short-lived individuals.

Model	Fixed effects	Random effects
1	Reproductive status + age + age^2	Year† + maternal ID‡
2	Reproductive status + age + age^2 + density + NAO	Year† + maternal ID‡
3	Reproductive status*age + Reproductive status*age^2 + density + NAO	Year† + maternal ID‡
4	Reproductive status*density + age + age^2 + NAO	Year† + maternal ID‡
5	Reproductive status*NAO + age + age^2 + density	Year† + maternal ID‡
6	Reproductive status*age*density + reproductive status*age^2*density + NAO	Year† + maternal ID‡
7	Reproductive status*age*NAO + reproductive status*age^2*NAO+ density	Year† + maternal ID‡
8	Reproductive status*density*NAO + age + age^2	Year† + maternal ID‡

† Year corresponds to the year when reproductive status was assigned when modelling over-winter survival, and the year of the reproductive event being modelled in the case of reproduction and twinning probability.

‡ Maternal ID was only included in models of reproduction and twinning probability.

3.4 Results

3.4.1 Over-winter survival

As in previous studies, we found evidence for significant survival costs of reproduction, with breeding individuals being less likely to survive the next winter (Table 3.3 - all survival models). We found some evidence that individuals that invested into lactation had greater survival costs than those that had not, given that females that had weaned at least one lamb were significantly less likely to survive than non-breeding females, whilst females that had given birth to a lamb, but had failed to wean it, were no less likely to survive than non-breeders (Table 3.3 - all survival models). Including variables describing individual resource acquisition and between-year variation in density and weather improved model fit regardless of which reproductive status measure was used in the analyses (Table 3.4 and Table 3.5). These models indicated that survival probability was higher for individuals of high adult body mass and lower when population density was high and winter weather was poor (Table 3.3 - model 3). Survival costs were evident when individual variation in resource acquisition and between-year environmental variation were absent from the model, with breeding individuals being 72% less likely to survive than individuals that did not breed and individuals that weaned a twin or weaned a singleton were 73% and 77% less likely to survive than individuals that did not breed (Table 3.3 - model 1). However, including data on individual variation in resource acquisition and between-year environmental variation resulted in more negative associations between breeding and survival probability. Individuals simply described as having bred were 79% less likely to survive than individuals that did not breed, whilst individuals that weaned a singleton and that weaned at least one twin were 84% and 89% less likely to survive than individuals that did not breed respectively (Table 3.3 - model 3). Nevertheless, it was apparent

that the decrease in the survival probability for these groups upon the inclusion of these terms was particularly driven by the inclusion of variables describing individual resource acquisition (Table 3.3 - model 2 versus model 3).

There was some evidence that the effect of reproductive status on survival varied with individual resource acquisition. The best fit model when reproductive status was defined to include variation in litter size and investment into lactation included an interaction between reproductive status and average adult body mass (Table 3.3 - best fit model). This term indicated that females that did not breed, that bred but did not wean a lamb, and that weaned a singleton, were more likely to survive if they were individuals that reached a high average adult body mass. In contrast, there was no variation in the survival probability of females that weaned at least one twin due to differences in average adult body mass, likely because only the heaviest females twin (Fig. 3.1). Furthermore, the best fit model using reproductive status when individuals were defined as simply bred or did not breed included an interaction between reproductive status, average adult body mass, and NAO, suggesting that the reduced survival of breeding individuals that were light as adults was most pronounced when winter conditions were harsh (Table 3.3). It is important to note that, although this model had the lowest AICc, there were four other models within 2 AICc units. This indicates that it was not clearly the best model and suggests that although winter conditions modify the effect of average adult body mass on the survival probability of breeding females, this effect is not particularly strong.

We did not find any evidence to suggest that the survival costs experienced by females varied with age, annual home range quality, population density, or NAO alone, given that the inclusion of first order interactions between reproductive status and each of these terms did not improve model fit (Table 3.4 and Table 3.5 - models 4-8). This was the case regardless of which reproductive status measure was used. NAO influenced the relationship between average adult body mass and

reproductive status when individuals were classified simply as having bred or not (Table 3.3 - best fit model). However, there was no evidence that age, average adult body mass, or annual home range quality influenced survival only when environmental conditions were poor (Table 3.4 and Table 3.5 - models 9-11 and 13-15).

Analyses conducted without measures of individual resource acquisition to include individuals that died early in life provided similar results. Increased investment into reproduction was associated with reduced over-winter survival, regardless of the reproductive status measure used, and this pattern was slightly more pronounced when accounting for between-year environmental variation (Table 3.6). The estimated reduction in survival probability for breeding individuals was less pronounced in these models than in those incorporating average adult body mass and home range quality. Furthermore, in these models, there was some evidence that the survival costs suffered by individuals varied with age, as the reduction in survival probability of old animals was greater when they invested more into reproduction (Table 3.6).

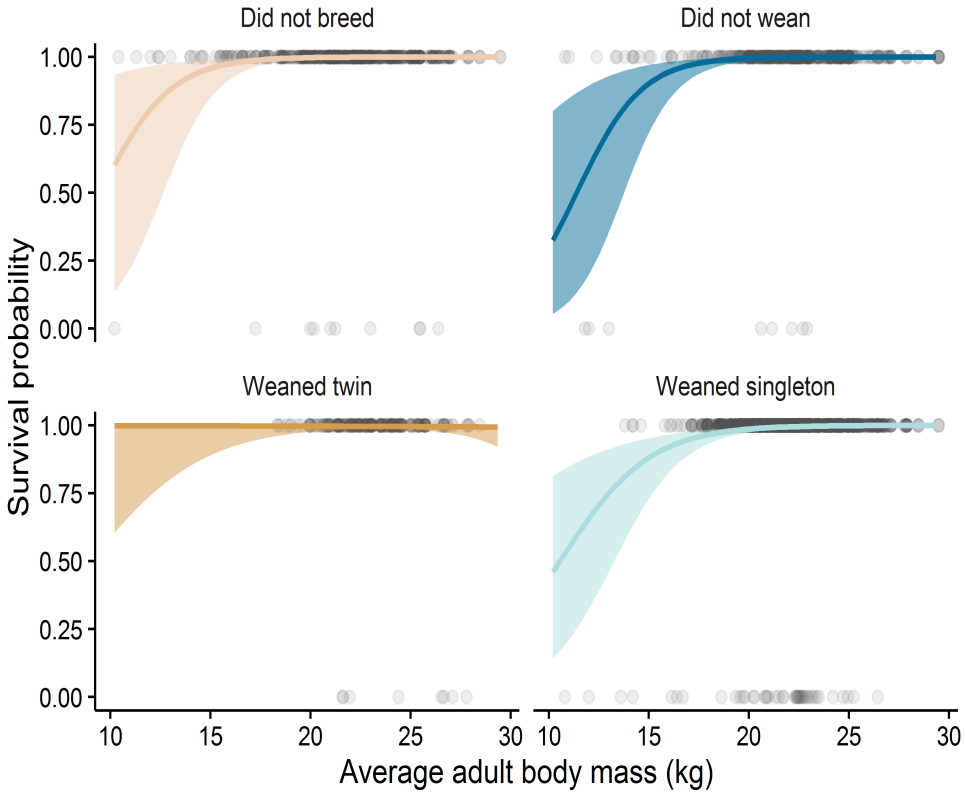

Figure 3.1: Female over-winter survival probability was higher for animals that reached high average adult body mass, except in the case of females that weaned at least one twin, with this likely to be driven by the fact that only the heaviest females twin. The regression line comes from model 5 (Table 3.1) which contained all main effects and an interaction between reproductive status and average adult body mass. The shaded regions represent 95% confidence intervals.

3.4.2 Future reproduction

We found little evidence that a female's investment into reproduction influenced the likelihood that she bred in the following year when using models including main effects only (Table 3.3 - models 1-3). These models suggested that individuals that bred in a given year were significantly more likely to reproduce the following year than individuals that did not breed, and that individuals that bred but did not wean their lamb(s), weaned a singleton, or weaned at least one twin, were all more likely to reproduce the following year than individuals that did not breed (Table 3.3). These results were consistent regardless of whether we accounted for

differences in average adult body mass, annual home range quality, population density, or NAO (Table 3.3 - models 1-3), in fact there was no evidence to suggest that an individual's probability of reproduction was influenced by population density or winter weather conditions (Table 3.4 and Table 3.5). There was also little evidence to suggest that the costs experienced by individuals in terms of reproduction were influenced by individual resource acquisition (no first order interactions included in the best model - Table 3.4 and Table 3.5, models 4-8), or variation in the environment between years (again, no first order interactions included in the best model - Table 3.4 and Table 3.5). However, the best fit model when using both definitions of reproductive status included an interaction between reproductive status, female age, and population density (Table 3.3). This interaction term suggests that, although old non-breeders were always less likely to reproduce the following year, old individuals that invested into reproduction in high density years were less likely to reproduce in a subsequent year than non-breeders (Fig. 3.2). Therefore, it seems that there is a cost in terms of the probability of reproducing the following year, but only for older females when the population density is particularly high.

Our analyses of future reproduction were generally consistent when we excluded average adult mass and annual home range quality. We found no evidence that females that invested more into reproduction were less likely to reproduce the following year when models included only main effects, regardless of the reproductive status used (Table 3.6). However, again the best fit model in both cases suggested that the probability of reproduction for old individuals that had invested a lot into their previous reproductive event was lower following a winter with a high population density (Table 3.6).

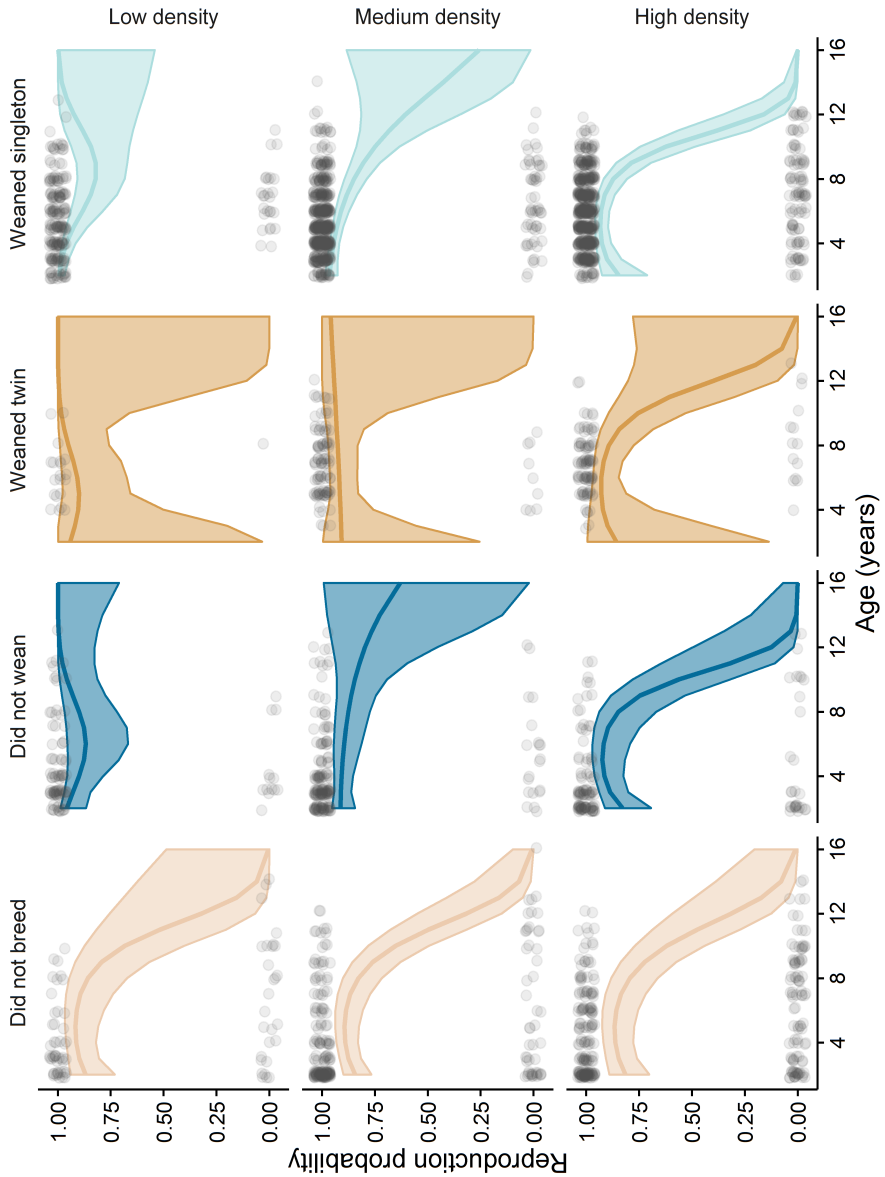

Figure 3.2: Old non-breeding individuals were always less likely to reproduce in the subsequent year, regardless of density, but old breeding individuals only showed reduced reproduction probability when density over the winter was high. The regression line comes from model 9 (Table 3.3) which contained all main effects and interactions between reproductive status, age, and population density. The shaded regions represent 95% confidence intervals.

Table 3.3: Parameter estimates and standard errors for models using reproductive status defined as a 4 level factor (Reproductive status A - did not breed, did not wean, weaned at least 1 twin, or weaned a singleton) or a 2 level factor (Reproductive status B - did not breed or bred). Presented are models 1 - 3 and the best fit model for the probability of over-winter survival, of reproduction in the following year, and of twinning in the subsequent year if a female successfully bred when variables describing individual variation in resource acquisition (body mass and home range quality) were included.

	Reproductive status A			Reproductive status B		
	Survival	Reproduction	Twinning	Survival	Reproduction	Twinning
Model 1						
intercept†	5.86^{***} (0.57)	1.50^{***} (0.21)	-2.72^{***} (0.26)	5.80^{***} (0.56)	-1.02 (0.55)	-9.77^{***} (0.98)
Status - did not wean	-0.88 (0.58)	0.43^{*} (0.21)	-0.08 (0.31)			
Status - weaned twin	-1.29^{*} (0.61)	0.89^{**} (0.30)	0.78^{*} (0.31)			
Status - weaned singleton	-1.47^{**} (0.49)	0.64^{***} (0.18)	0.25 (0.24)			
Status - bred				-1.29^{**} (0.46)	0.58^{***} (0.17)	0.26 (0.24)
Age	0.29 (0.56)	1.21^{***} (0.32)	3.25^{***} (0.50)	0.13 (0.53)	0.47^{***} (0.10)	1.27^{***} (0.17)
Age^2	-1.31^{**} (0.46)	-1.81^{***} (0.32)	-2.73^{***} (0.51)	-1.17^{**} (0.44)	-1.95^{***} (0.31)	-3.11^{***} (0.50)
Model 2						
intercept†	6.69^{***} (0.64)	1.50^{***} (0.21)	-2.73^{***} (0.26)	6.51^{***} (0.62)	-0.92 (0.55)	-9.58^{***} (0.97)
Status - did not wean	-0.77 (0.61)	0.42^{*} (0.21)	-0.15 (0.31)			
Status - weaned twin	-2.15^{***} (0.65)	0.83^{**} (0.30)	0.74^{*} (0.31)			
Status - weaned singleton	-1.78^{***} (0.51)	0.63^{***} (0.18)	0.18 (0.24)			
Status - bred				-1.50^{**} (0.47)	0.56^{***} (0.17)	0.19 (0.24)
Age	0.19 (0.58)	1.17^{***} (0.32)	3.13^{***} (0.49)	-0.16 (0.55)	0.45^{***} (0.10)	1.24^{***} (0.17)
Age^2	-1.77^{***} (0.48)	-1.82^{***} (0.32)	-2.73^{***} (0.50)	-1.44^{**} (0.45)	-1.95^{***} (0.31)	-3.11^{***} (0.50)
Body mass	1.38^{***} (0.18)	0.19^{*} (0.08)	0.55^{***} (0.13)	1.29^{***} (0.17)	0.20^{*} (0.08)	0.59^{***} (0.14)
Home range quality	0.12 (0.16)	0.08 (0.08)	0.22^{*} (0.10)	0.10 (0.16)	0.08 (0.08)	0.23^{*} (0.10)
Model 3						
intercept†	6.65^{***} (0.56)	1.49^{***} (0.21)	-2.79^{***} (0.24)	6.48^{***} (0.54)	-0.99 (0.55)	-9.87^{***} (0.98)
Status - did not wean	-0.83 (0.59)	0.40 (0.21)	-0.26 (0.31)			
Status - weaned twin	-2.17^{***} (0.63)	0.83^{**} (0.30)	0.75^{*} (0.31)			
Status - weaned singleton	-1.82^{***} (0.49)	0.62^{***} (0.18)	0.15 (0.24)			
Status - bred				-1.55^{***} (0.46)	0.55^{***} (0.17)	0.16 (0.24)
Age	0.27 (0.58)	1.20^{***} (0.32)	3.21^{***} (0.49)	-0.10 (0.54)	0.46^{***} (0.11)	1.28^{***} (0.17)
Age^2	-1.78^{***} (0.48)	-1.83^{***} (0.32)	-2.78^{***} (0.49)	-1.44^{**} (0.44)	-1.97^{***} (0.31)	-3.21^{***} (0.49)
Body mass	1.34^{***} (0.18)	0.18^{*} (0.08)	0.52^{***} (0.13)	1.26^{***} (0.17)	0.19^{*} (0.08)	0.56^{***} (0.14)
Home range quality	0.11 (0.15)	0.08 (0.08)	0.22^{*} (0.10)	0.10 (0.15)	0.09 (0.08)	0.24^{*} (0.10)
Density	-1.08^{***} (0.25)	-0.22 (0.14)	-0.46^{***} (0.09)	-1.08^{***} (0.24)	-0.22 (0.14)	-0.44^{***} (0.09)
NAO	-1.28^{***} (0.25)	0.06 (0.13)	-0.11 (0.08)	-1.23^{***} (0.25)	0.06 (0.13)	-0.10 (0.08)
Best fit model						
intercept†	6.82^{***} (0.60)	1.56^{***} (0.22)	-2.79^{***} (0.24)	7.01^{***} (0.72)	-1.30 (0.89)	-9.87^{***} (0.98)
Status - did not wean	-0.57 (0.71)	0.42 (0.24)	-0.26 (0.31)			

Status - weaned twin	−1.50 (0.82)	0.72 (0.58)	0.75* (0.31)			
Status - weaned singleton	−1.95*** (0.54)	0.68*** (0.19)	0.15 (0.24)			
Status - bred				−2.14** (0.67)	1.76 (1.18)	0.16 (0.24)
Age	−0.03 (0.61)	1.53** (0.51)	3.21*** (0.49)	−0.05 (0.57)	0.53** (0.17)	1.28*** (0.17)
Age^2	−1.58** (0.50)	−2.12*** (0.53)	−2.78*** (0.49)	−1.47** (0.47)	−2.12*** (0.52)	−3.21*** (0.49)
Body mass	1.64*** (0.32)	0.16* (0.09)	0.52*** (0.13)	1.10* (0.51)	0.18* (0.09)	0.56*** (0.14)
Home range quality	0.08 (0.16)	0.08 (0.08)	0.22* (0.10)	0.09 (0.16)	0.09 (0.08)	0.24* (0.10)
Density	−1.05*** (0.25)	−0.16 (0.17)	−0.46*** (0.09)	−1.13*** (0.23)	0.07 (0.91)	−0.44*** (0.09)
NAO	−1.29*** (0.25)	0.06 (0.13)	−0.11 (0.08)	−1.77** (0.60)	0.06 (0.13)	−0.10 (0.08)
Status - did not wean:body mass	0.14 (0.42)					
Status - weaned twin:body mass	−1.87** (0.69)					
Status - weaned singleton:body mass	−0.34 (0.36)					
Status - bred:body mass				0.004 (0.53)		
Status - did not wean:age		−0.63 (0.96)				
Status - weaned twin:age		−0.84 (2.58)				
Status - weaned singleton:age		−1.09 (0.77)				
Status - bred:age					−0.22 (0.22)	
Status - did not wean:age^2		0.77 (1.00)				
Status - weaned twin:age^2		1.36 (2.46)				
Status - weaned singleton:age^2		0.85 (0.76)				
Status - bred:age^2					0.61 (0.65)	
Status - did not wean:density		−0.16 (0.21)				
Status - weaned twin:density		−0.15 (0.54)				
Status - weaned singleton:density		−0.25 (0.18)				
Status - bred:density					−4.20*** (1.21)	
Age:density		−0.12 (0.50)			−0.04 (0.17)	
Age^2:density		0.16 (0.52)			0.16 (0.52)	
Status - did not wean:age:density		2.16* (1.01)				
Status - weaned twin:age:density		1.68 (2.29)				
Status - weaned singleton:age:density		2.65*** (0.78)				
Status - bred:age:density					0.75*** (0.22)	
Status - did not wean:Age^2:density		−2.61* (1.08)				
Status - weaned twin:Age^2:density		−2.19 (2.16)				
Status - weaned singleton:Age^2:density		−2.65*** (0.79)				
Status - bred:Age^2:density					−2.34*** (0.67)	
Body mass:NAO				0.74 (0.49)		
Status - bred:NAO				0.69 (0.62)		
Status - bred:body mass:NAO				−0.35 (0.54)		

*p<0.1; **p<0.05; ***p<0.01

† the reproductive status 'did not breed' is the reference level

3.4.3 Twinning

We also found that females that had invested more into reproduction in a given year did not experience a cost in terms of their probability to produce twin litters in the subsequent year. When assigning females as having bred or not bred, there was no evidence that reproductive status in a given year was associated with a difference in twinning probability the next year (Table 3.3 - all twinning models). When using the alternative definition of reproductive status, we found that females that did not wean a lamb, or weaned a singleton lamb were no more likely to twin than individuals that did not breed, but that females that weaned at least one twin were more likely to bear twins in the following year (Table 3.3 - all twinning models). Incorporating data on average adult body mass and annual home range quality improved model fit (Table 3.4 and Table 3.5 - model 2) and showed that twinning probability was higher for individuals that reached a higher adult body mass and for individuals with higher quality annual home ranges. However, including these terms resulted in only a small change in the parameter estimates for the effects of the different reproductive statuses (Table 3.3 - model 2). The same was true for population density and NAO. The inclusion of these variables improved model fit in both cases, but resulted in little change in the estimated effects of differing levels of reproductive investment (Table 3.3 - model 3). In both cases the best fit model was model 3, suggesting that the effect of reproductive investment on twinning probability was not influenced by differences in resource acquisition or environmental conditions. Models excluding average adult body mass and annual home range quality produced similar results, suggesting that increased investment into reproduction was not associated with a reduction in twinning probability (Table 3.6).

Table 3.4: AICc values for all models used in the analysis of survival, reproduction and twinning probability when reproductive status was defined as a 4 level factor (did not breed, bred but did not wean lamb(s), weaned at least 1 twin, or weaned a singleton). Shown are AICc values for models when both body mass and home range quality were included and excluded (with resource acquisition and without resource acquisition respectively). The AICc of the best fit model in each case is shown in bold.

	With resource acquisition			Without resource acquisition		
Model	Survival	Reproduction	Twinning	Survival	Reproduction	Twinning
1	500.9809	2130.372	1672.591	645.5399	2490.004	1836.552
2	437.4053	2128.236	1652.503	623.1749	2492.335	**1816.133**
3	422.002	2129.164	**1634.083**	**622.776**	2496.243	1821.255
4	428.5184	2134.572	1637.155	624.5759	2494.932	1819.47
5	**417.5502**	2129.089	1638.837	626.7382	2496.462	1821.567
6	426.5747	2129.852	1637.554	627.9911	**2480.108**	1822.065
7	425.7531	2133.599	1638.217	636.1246	2505.733	1828.209
8	426.8711	2134.701	1638.04	628.676	2506.58	1829
9	433.4623	**2120.649**	1640.19			
10	440.9086	2147.533	1643.699			
11	425.1464	2137.143	1648.575			
12	422.1024	2138.202	1646.418			
13	434.194	2140.844	1648.609			
14	430.5781	2135.953	1646.385			
15	434.8043	2142.343	1648.081			

Table 3.5: AICc values for all models used in the analysis of survival, reproduction and twinning probability when reproductive status was defined as a 2 level factor (did not breed or bred). Shown are AICc values for models when both body mass and home range quality were included and excluded (with resource acquisition and without resource acquisition respectively). The AICc of the best fit model in each case is shown in bold.

	With resource acquisition			Without resource acquisition		
Model	Survival	Reproduction	Twinning	Survival	Reproduction	Twinning
1	498.8081	2128.784	1676.043	642.5626	2489.076	1837.182
2	438.8132	2126.203	1656.618	620.3526	2491.487	1818.325
3	423.4257	2127.274	**1640.641**	**615.5820**	2493.953	1822.148
4	425.5799	2131.087	1644.676	621.3890	2491.729	1820.159
5	424.1448	2126.617	1642.628	620.0430	2491.784	1820.130
6	425.0075	2128.240	1641.157	615.8466	**2470.785**	1825.570
7	425.4374	2129.210	1642.519	647.1152	2492.682	**1817.297**
8	424.7947	2128.854	1641.480	622.9586	2495.894	1820.966
9	426.1201	**2110.389**	1648.506			
10	431.8307	2132.968	1641.492			
11	429.9617	2128.003	1648.055			
12	**423.2196**	2128.568	1646.551			
13	428.4233	2133.254	1645.097			
14	429.5108	2126.999	1643.060			
15	428.8817	2131.544	1644.805			

Table 3.6: Parameter estimates and standard errors for models using reproductive status defined as a 4 level factor (Reproductive status A - did not breed, did not wean, weaned at least 1 twin, or weaned a singleton) or a 2 level factor (Reproductive status B - did not breed or bred). Presented are models 1 - 3 and the best fit model for the probability of over-winter survival, of reproduction in the following year, and of twinning in the subsequent year if a female successfully bred when average adult body mass and annual home range quality were excluded.

	Reproductive status A			Reproductive status B		
	Survival	Reproduction	Twinning	Survival	Reproduction	Twinning
Model 1						
intercept†	5.08^{***} (0.46)	1.27^{***} (0.20)	-2.76^{***} (0.25)	5.06^{***} (0.46)	-1.28^{*} (0.52)	-9.64^{***} (0.93)
Status - did not wean	-0.65 (0.44)	0.57^{**} (0.19)	-0.07 (0.30)			
Status - weaned twin	-0.93 (0.53)	1.06^{***} (0.29)	0.60^{*} (0.30)			
Status - weaned singleton	-1.02^{**} (0.37)	0.83^{***} (0.17)	0.26 (0.23)			
Status - bred				-0.90^{**} (0.35)	0.74^{***} (0.16)	0.24 (0.23)
Age	1.29^{**} (0.45)	1.22^{***} (0.30)	3.28^{***} (0.48)	1.15^{**} (0.42)	0.48^{***} (0.10)	1.25^{***} (0.16)
Age ^{2}	-1.91^{***} (0.39)	-1.81^{***} (0.31)	-2.75^{***} (0.49)	-1.80^{***} (0.37)	-1.97^{***} (0.30)	-3.05^{***} (0.48)
Model 2						
intercept†	5.12^{***} (0.36)	1.26^{***} (0.19)	-2.81^{***} (0.24)	5.08^{***} (0.36)	-1.33^{*} (0.52)	-9.89^{***} (0.93)
Status - did not wean	-0.73 (0.44)	0.56^{**} (0.19)	-0.17 (0.29)			
Status - weaned twin	-0.99 (0.52)	1.05^{***} (0.29)	0.58^{*} (0.29)			
Status - weaned singleton	-1.12^{**} (0.37)	0.82^{***} (0.17)	0.23 (0.23)			
Status - bred				-1.00^{**} (0.35)	0.73^{***} (0.16)	0.20 (0.22)
Age	1.44^{**} (0.44)	1.24^{***} (0.30)	3.36^{***} (0.48)	1.30^{**} (0.41)	0.49^{***} (0.10)	1.29^{***} (0.16)
Age ^{2}	-2.03^{***} (0.39)	-1.82^{***} (0.31)	-2.81^{***} (0.48)	-1.91^{***} (0.36)	-1.98^{***} (0.30)	-3.14^{***} (0.47)
Density	-1.19^{***} (0.20)	-0.12 (0.12)	-0.47^{***} (0.08)	-1.19^{***} (0.20)	-0.12 (0.12)	-0.45^{***} (0.09)
NAO	-1.13^{***} (0.19)	0.08 (0.12)	-0.10 (0.08)	-1.12^{***} (0.18)	0.08 (0.12)	-0.09 (0.08)
Best fit model						
intercept†	4.74^{***} (0.35)	1.35^{***} (0.21)	-2.81^{***} (0.24)	4.74^{***} (0.35)	-1.78^{*} (0.81)	-9.57^{***} (2.04)
Status - did not wean	-0.22 (0.52)	0.51^{*} (0.22)	-0.17 (0.29)			
Status - weaned twin	-0.16 (1.22)	0.97 (0.56)	0.58^{*} (0.29)			
Status - weaned singleton	-0.64 (0.37)	0.84^{***} (0.18)	0.23 (0.23)			
Status - bred				-0.58 (0.35)	2.27^{*} (1.11)	-1.06 (2.30)
Age	1.33 (0.70)	1.65^{***} (0.47)	3.36^{***} (0.48)	1.33 (0.70)	0.58^{***} (0.16)	1.22^{***} (0.37)
Age^{2}	-1.61^{**} (0.58)	-2.16^{**} (0.49)	-2.81^{***} (0.48)	-1.61^{**} (0.58)	-2.19^{***} (0.49)	-2.99^{*} (1.18)
Density	-1.19^{***} (0.20)	0.03 (0.16)	-0.47^{***} (0.08)	-1.20^{***} (0.20)	-0.37 (0.83)	-0.47^{***} (0.09)
NAO	-1.17^{***} (0.18)	0.08 (0.12)	-0.10 (0.08)	-1.13^{***} (0.18)	0.08 (0.12)	4.22^{*} (2.14)
Status - did not wean:age	0.98 (1.39)	-1.28 (0.89)				
Status - weaned twin:age	0.60 (3.26)	-0.98 (2.54)				
Status - weaned singleton:age	0.21 (0.97)	-0.99 (0.72)				
Status - bred:age				0.34 (0.85)	-0.28 (0.21)	0.23 (0.41)

Status - did not wean:age^2	−1.13 (1.28)	1.30 (0.94)			
Status - weaned twin:age^2	−1.37 (2.44)	1.40 (2.42)			
Status - weaned singleton:age^2	−0.77 (0.84)	0.72 (0.72)			
Status - bred:age^2			−0.81 (0.73)	0.73 (0.62)	−0.68 (1.32)
Status - did not wean:density		−0.30 (0.20)			
Status - weaned twin:density		−0.36 (0.52)			
Status - weaned singleton:density		−0.36* (0.16)			
Status - bred:density				−3.73*** (1.13)	
Age:density		0.22 (0.46)		0.07 (0.16)	
Age^2:density		−0.24 (0.48)		−0.23 (0.48)	
Status - did not wean:age:density		1.99* (0.92)			
Status - weaned twin:age:density		1.25 (2.26)			
Status - weaned singleton:age:density		2.20** (0.72)			
Status - bred:age:density				0.64** (0.21)	
Status - did not wean:age^2:density		−2.35* (1.00)			
Status - weaned twin:age^2:density		−1.58 (2.11)			
Status - weaned singleton:age^2:density		−2.15** (0.74)			
Status - bred:age^2:density				−1.94** (0.63)	
Status - bred:NAO					−5.77* (2.39)
Age:NAO					−0.79* (0.38)
Age^2:NAO					3.17* (1.30)
Status - bred:age:NAO					1.04* (0.43)
Status - bred:age^2:NAO					−4.16** (1.42)

*p<0.05; **p<0.01; ***p<0.001

† the reproductive status 'did not breed' is the reference level

3.5 Discussion

Here we examined the effect of variation in individual resource acquisition and in environmental conditions on the cost of reproduction experienced by female Soay sheep. Our work adds to our understanding of the context-dependence of the cost of reproduction by adding information on individual home range qualities to understand how an individual's access to resources, alongside variation in resource acquisition due to differences in average adult body mass, influenced survival and reproductive costs. There has been little attempt to incorporate variation in space use into analyses of reproductive costs, likely because it is often difficult to obtain sufficient data within the long-term studies that provide the necessary life-history data. Nevertheless, describing an individual's use of space will be necessary to better describe variation between individuals with respect to resource acquisition and therefore understand how differences in resource acquisition influence life-history trade-offs. Although we found that survival costs were more pronounced when individual and environmental variation were accounted for, we found no evidence that an individual's home range quality influenced the costs they experienced as a result of reproduction, as the interaction between reproductive status and annual home range quality was absent from all best fit models. However, we did find that access to home ranges with high quality vegetation influenced individual life history, particularly in the case of twinning probability. It was apparent that the likelihood of a female giving birth to twins was significantly higher if she had a high quality home range in the previous year. An individual's access to resources is likely to influence reproductive success by determining the energy available for investment into life history traits and relationships between habitat use or selection have been shown for red deer (McLoughlin et al. 2006), roe deer (Mcloughlin et al. 2007), and Soay sheep (Regan et al. 2016). Indeed, the increased lifetime reproductive success for female Soay sheep with high quality

home ranges may, to some extent, have been mediated by the relationship between home range quality and twinning probability that we have demonstrated here.

There are a number of potential causes for the lack of a relationship between an individual's home range quality and the costs they experience as a result of reproduction, though future work will be needed to address this issue. There is evidence to suggest that resources in Village Bay are not limiting over the summer (Crawley et al. 2004) and therefore females with very different home range qualities may be able to access similar levels of nutrition during this period. Our work therefore shows the importance of understanding the ways in which individuals obtain the resources necessary for reproduction. Understanding how individuals finance reproduction, for example whether they are a capital versus income breeder and therefore rely more on stored resources, is likely to be important when considering the best ways to quantity resource access. Similarly, measures of habitat quality are specific to particular spatial scales and it is possible that a measure of quality at a different spatial scale may better explain variation in survival and/or reproduction (Gaillard et al. 2010). For example, the mean percentage cover of *H. lanatus* provides information on individual access to the *Holcus-Agrostis* grassland that is preferred by the sheep (Jones 2003), but it may be that variation in vegetation availability/quality at finer spatial scales (e.g. the availability of gaps versus tussocks (Hutchings et al. 2002)) is important in determining individual energy intake. Finally, it is possible that the average percentage cover used in our study does not capture the full degree of variation in resource access between individuals and may necessitate the use of other measures of resource access.

We found that the probability of over-winter survival and reproduction in the subsequent year were affected by population density and winter NAO. As in previous studies (Clutton-Brock et al. 1996; Tavecchia et al. 2005) there was evidence for significant survival costs of reproduction for female Soay sheep.

Breeding females were less likely to survive the winter than non-breeding females, and more specifically, individuals that weaned a singleton or at least one twin and had therefore invested more into lactation, experienced significantly reduced survival when compared with individuals that had not bred. On the other hand, females that had given birth to a lamb (or lambs) but had not weaned them, were not significantly more likely to die during the subsequent winter when compared with non-breeders. Together these results suggest that lactation is particularly costly. In contrast to previous work (Clutton-Brock et al. 1996; Tavecchia et al. 2005), we did find some evidence for costs in terms of the probability of an individual reproducing in the following year, but these were less marked than survival costs as they were only evident for old animals breeding in high density years. Such an effect of density and NAO on the cost of reproduction is perhaps unsurprising because population density and winter weather are known to influence many aspects of Soay sheep biology, including lamb birth dates, birth weights (Forchhammer et al. 2001), early growth (Ozgul et al. 2009), female age at first reproduction (Forchhammer et al. 2001; Tavecchia et al. 2005), and the over-winter survival of both males and females (Milner et al. 1999; Catchpole et al. 2000). However, our results contrast slightly with previous studies, which suggested that the increased survival cost given harsh conditions was most pronounced for young and old breeding individuals (Clutton-Brock et al. 1996; Tavecchia et al. 2005). However, we note that Clutton-Brock et al. (1996) also suggested that the survival costs of reproduction were greater for lighter individuals in years where environmental conditions were poor. It is difficult to directly compare these studies given differences in the amount of data available, the way in which environmental conditions were characterised (e.g. Tavecchia et al. (2005) separated years based on a combination of density and NAO and Clutton-Brock et al. (1996) divided years into those that were crash and non-crash), and differences in statistical approaches, but the fact that the general conclusions are comparable suggests that our results

are robust.

We found that survival costs were more pronounced when individual and environmental variation were accounted for and that a cost in terms of future reproduction was only apparent once relationships between reproductive status, age, and population density were included in the model. This finding somewhat supports the idea that differences between individuals in their access to resources might provide an explanation for the lack of costs of reproduction in many studies of wild animal populations (van Noordwijk and de Jong 1986; Hamel et al. 2010a). Our results suggest that female Soay sheep experience far more substantial costs in terms of reduced future survival than in terms of future reproductive output, at least given the ways in which we quantified future reproductive output. It is important to consider that the manner in which costs of reproduction are expressed is expected to vary between species given the wide variation in life history strategies (Hamel et al. 2010b). For example, long-lived species, such as Soay sheep, are expected to invest more resources into survival than reproduction because their fitness is determined to a greater degree by their own survival, with the opposite being true for short-lived species (Gaillard and Yoccoz 2003). As a result, in long-lived species the variance in reproductive output is expected to be higher than for survival, whilst short-lived species are expected to show more variation in terms of survival (Gaillard et al. 1998; Gaillard and Yoccoz 2003).

The difference between species with fast and slow life-history strategies, in terms of whether survival or reproduction is more variable, led Hamel et al. 2010b to suggest that reproductive costs should be more likely in the fitness component with the higher variance. Ungulates, which are relatively long-lived and expected to follow a slow life-history strategy, are predicted to show more variable reproduction than survival, suggesting that we should expect more frequently to observe costs in terms of future reproduction (Hamel et al. 2010b). Such a trend is supported by the literature, with Hamel et al. (2010b) finding that a greater

proportion of ungulate studies have found evidence for reductions in future reproduction than studies conducted on rodents, whilst the opposite is true for survival costs. Given that Soay sheep are relatively long-lived and are therefore expected to follow a conservative reproductive strategy in which they favour their own survival, we would expect to find evidence for reproductive rather than survival costs. In fact, we find the opposite result, with Soay sheep experiencing greater costs in terms of future survival than in terms of future reproduction. A potential explanation for this may lie in the somewhat unusual biology of the Soay sheep. The Hirta population occasionally experiences crashes, in which up to 70% of the population dies, that are driven by density, weather, and the population's age and sex structure (Coulson et al. 2001; Clutton-Brock et al. 2004). Females do not seem to be able to predict such events, and adjust their investment into reproduction based on their current body mass and age (Clutton-Brock et al. 1996) rather than density. As a result, the reproductive output of adult females is relatively constant, with the majority of ewes breeding each year, whilst mortality can vary markedly between years (Clutton-Brock et al. 1996). Therefore, survival costs are likely to be more prevalent than costs in terms of future reproduction in this relatively long-lived species.

Studying life-history trade-offs, such as the cost of reproduction, is complicated for many reasons, particularly as we strive to account for multiple sources of individual and environmental variation. Characterising individual heterogeneity can be difficult, with substantial debate surrounding the ways in which individual quality can be defined and how it should best be incorporated into analyses within evolutionary ecology (Wilson and Nussey 2010). Wilson and Nussey (2010) suggest that multivariate approaches to characterising quality are preferable to using single traits because individual indicators of quality might only be weakly correlated, making it difficult to justify the selection of a single trait. They therefore propose a way in which multiple candidate traits can be used to derive a measure of

phenotypic variation that best explains variance in fitness (Wilson and Nussey 2010). One factor that can complicate the characterisation of a measure of quality, even using the approach proposed by Wilson and Nussey (2010), is the lack of phenotypic data for certain groups of animals that are likely to be a non-random subset of the population in terms of fitness. For example, in our case, many short-lived animals lacked data on body mass and body size. It may be possible to get around this problem by accounting for individual heterogeneity without using data for specific traits believed to be associated with fitness allowing us to get around this problem. For example, Garnier et al. (2016) used mixture models to account for unmeasured individual heterogeneity that resulted in two types of coexisting females, one which had high probabilities of both survival and recruitment and one which had low probabilities of survival and recruitment. Although this approach allows you to account for unmeasured variation between individuals when studying trade-offs using capture-mark-recapture models, it has its limitations given that it is not possible to draw any conclusions about the source of the identified individual heterogeneity. Therefore, it will be difficult to assess the potential evolutionary consequences of any identified costs from such models as it becomes impossible to assess the genetic or environmental determinants of such quality variation. Capture-mark-recapture analyses are commonly used to study the cost of reproduction (e.g. Tavecchia et al. (2001); Barbraud and Weimerskirch (2005); Moyes et al. (2006); Lescroël et al. (2009)) as they make it possible to account for variation in recapture probability within specific groups of animals, and more recently multi-event capture-mark-recapture models have even made it possible to account for uncertainty when assigning reproductive states (Pradel 2005). Though such an approach can be particularly useful when detection probability is low or reproductive status is determined in such a way that maternities may be wrongly assigned (e.g. limited observations), we believe that little bias is unlikely to have been introduced to our analyses as a

result of not using these models. This is because the recapture probability of both breeding and non-breeding animals post-2000 was 1 and a combination of intensive searches and genetic maternity assignment mean that reproductive status is assigned with very high accuracy in the Soay sheep.

There is substantial scope for further studies surrounding the cost of reproduction in this and other populations. In particular, it may prove fruitful to examine the costs in relation to additional definitions of reproductive investment that cover a more complete range of possible situations. For example, to truly understand the contributions of gestation versus lactation to the costs experienced by individuals it would be useful to be able to separate individuals based on the length of time they gestated a lamb or the time over which they provided milk, particularly given that the latter portion of gestation and the early lactation period are the most energetically costly (Mauget et al. 1999). Furthermore, there is still a need to investigate the effect of the social environment on life-history trade-offs, particularly in species where there is pronounced social structure. Many studies have accounted for variation in density, but little attention has been paid to other aspects of the social environment, such as group composition or sex ratio (but see Nicolaus et al. 2012 and Debeffe et al. 2017). Therefore, additional work will be needed to better understand the influence of social effects on life-history trade-offs. Similarly, we believe there is still substantial scope to understand how an individual's access to resources influences investment into competing life-history traits, and the degree to which animals may adjust their foraging behaviour accordingly. It is clear that it is likely to be difficult to accurately characterise the resources available to individuals over the most appropriate time scale for the trait(s) in question and, as such, work examining the effect of spatial and temporal scale within such studies will provide invaluable guidance.

Chapter 4

Accounting for female space sharing in St. Kilda Soay sheep (*Ovis aries*) results in little change in heritability estimates

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4.1 Abstract

When estimating heritability in free-living populations, it is common practice to account for common environment effects, because of their potential to generate phenotypic covariance among relatives thereby biasing heritability estimates. In quantitative genetic studies of natural populations, however, philopatry, which results in relatives being clustered in space, is rarely accounted for. The two studies to have done so suggest absolute declines in heritability estimates of up to 43% when accounting for space sharing by relatives. However, due to methodological limitations these estimates may not be representative. We used data from the St. Kilda Soay sheep population to estimate heritabilities with and without accounting for space sharing for five traits for which there is evidence for additive genetic variance (birth weight, birth date, lamb August weight, and female post mortem jaw and metacarpal length). We accounted for space sharing by related females by separately incorporating spatial autocorrelation, and a home range similarity matrix. Although these terms accounted for up to 17% of the variance in these traits, heritability estimates were only reduced by up to 7%. Our results suggest that the bias caused by not accounting for space sharing may be lower than previously thought. This suggests that philopatry does not inevitably lead to a large bias if space sharing by relatives is not accounted for. We hope our work stimulates researchers to model shared space when relatives in their study population share space, as doing so will enable us to better understand when bias may be of particular concern.

4.2 Introduction

Animal breeders and evolutionary biologists often want to estimate a trait's evolutionary potential. To do this, we estimate genetic components of variance for,

and covariance between, traits of interest. In the simplest univariate case, studies typically focus on the additive genetic variance (V_A) and narrow-sense heritability (h^2, the ratio of V_A to phenotypic variance). Through quantitative genetic models, these parameters can be estimated for quantitative traits using data on the phenotypic similarities of individuals of known relatedness (Falconer and Mackay 1996; Lynch and Walsh 1998). The development of the 'animal model', a type of mixed effects model, has greatly advanced the application of quantitative genetic analysis to wild populations. This is because the animal model uses information from individuals of varying degrees of relatedness, can cope with missing links in the complex pedigrees so typical of wild populations, and is flexible enough to incorporate known or hypothesised non-genetic influences on the phenotype (Wilson et al. 2010). Non-genetic influences on the phenotype can come from a variety of sources. In general, if environmental conditions affect phenotypes, then individuals that share a similar environment will have similar phenotypes (but note that there are exceptions: for example, sibling competition can generate greater within-brood variation in growth and survival (Nilsson and Svensson 1996). Environmental effects that are shared by groups of individuals are referred to as 'common environment' effects (Falconer and Mackay 1996), and these effects generate increased phenotypic similarity. In experimental studies, it is standard practice to break up the association between genes and the local environment by distributing families across, for example, cages or tanks. Such an approach is not generally feasible in the wild, and therefore statistical techniques are used to account for common environment effects (e.g. birth year or habitat type) by including them as fixed or random effects (e.g. McCleery et al. 2004; Vergara et al. 2015). Cross-fostering has however been used to separate out environmentally derived similarity from that due to shared genes in some studies of birds (Hadfield et al. 2006), and mammals (McAdam et al. 2002). A combination of cross-fostering and the animal model is the best way to avoid bias in genetic parameters when

common environment effects are strong (Kruuk and Hadfield 2007), however cross-fostering is not feasible in all systems used to study quantitative genetics in the wild, for example the ungulates.

Relatives are often clustered in time and/or space, and therefore often share environments as well as genes. Where this is the case, common environment effects can be particularly problematic, resulting in biased heritability estimates because we make the mistake of assuming that their similarity is due to shared genes alone (Kruuk and Hadfield 2007). For example, maternal effects result in offspring born to the same mother being more similar to one another than offspring from different mothers (Falconer and Mackay 1996). Therefore, failing to account for maternal effects can upwardly bias estimates of V_A, and consequently h^2 (Wilson et al. 2005). As a result, it is now routine to account for maternal effects when conducting quantitative genetic analysis. Other sources of common environment effects however have received less attention in quantitative genetic analyses of natural populations. For example, we tend to neglect the fact that relatives can experience similar environments even into adulthood, as a result of natal philopatry (e.g. Rossiter et al. (2002)). If this is the case, and the environment is spatially heterogeneous, then we might expect relatives to be more phenotypically similar, because they experience more similar environments. In other words, the value of a trait expressed in an individual may be related to the trait values of individuals at nearby locations, a phenomenon known as spatial autocorrelation (SAC) (Cliff and Ord 1981; Olalla-Tárraga et al. 2007; Ng et al. 2013). As with maternal effects, failing to account for this type of common environment effect has the potential to bias estimates of V_A and h^2. The potential for SAC to be a source of bias in genetic parameter estimates has been of concern to plant breeders for some time (Cullis and Gleeson 1989, 1991; Magnussen 1993; Qiao et al. 2000), particularly in the case of forestry and agricultural variety trials (Dutkowski et al. 2002). Traditionally, experimental design was used to combat this problem, but was often

unsuccessful because of the variability in the patterns and scale of spatial variation, resulting from differences in the underlying gradients, ranging from soil and microclimatic effects, to cultural and measurement effects (Dutkowski et al. 2002). Statistical techniques to explicitly model SAC in analyses primarily aimed at estimating genetic parameters have therefore become more popular (Dutkowski et al. 2002). Though the addition of an SAC term generally results in model improvement, the effect of doing so on the genetic variance is variable, with both increases and decreases reported in the plant breeding and forestry literature (Silva et al. 2001; Dutkowski et al. 2002, 2006; Banerjee et al. 2010).

Although studies on plants illustrate that accounting for spatial sources of similarity can be important in deriving accurate heritability estimates, to our knowledge there have only been two studies that have considered space sharing by relatives beyond the immediate natal environments when conducting quantitative genetic studies on wild animal populations (but see Heckerman et al. 2016 for a recent human study). Firstly, a study of laying date and clutch size in the Wytham wood great tit (*Parus major*) population, found that accounting for SAC resulted in an absolute decrease of 25% (from 40% to 15%) in the estimated heritability of laying date, though no such trend was evident for clutch size (Van Der Jeugd and McCleery 2002). Secondly, a study on the red deer (*Cervus elaphus*) population on the Scottish island of Rum found evidence consistent with space sharing being an important source of bias in heritability estimates (Stopher et al. 2012). In this study, the change in the estimated heritability varied substantially, from an absolute change of 43% (from 44% to <1%) in the case of spring home range size to only around 4% for lifetime breeding success (from 4% to <1%) (Stopher et al. 2012). Although these studies have greatly advanced our understanding of how failure to account for spatial structure in wild populations may bias heritability estimates, there is a need to build on these works, using improved methodologies to understand how heritability estimates are affected when space sharing by relatives

is not or cannot be accounted for. Firstly, we need to continue to develop methods to account for space sharing within the animal model, given that heritability estimates derived from out-dated techniques, such as parent-offspring regression are less accurate (Kruuk 2004; Akesson et al. 2008). Of the two studies mentioned above, only the one by Stopher et al. (2012) used the animal model approach, while Van Der Jeugd and McCleery (2002) conducted parent-offspring regressions for three groups of individuals whose nestboxes were separated by varying distances. The extension of this approach to additional traits, populations and species will be necessary before there can be any general conclusions about the effect of accounting for space sharing by relatives on heritability estimates. Secondly, we need to make use of the sophisticated methods available to quantify individual space use, such as utilisation distributions (UDs - a relative frequency distribution describing the probability of an individual occurring at a particular location at a specific point in time) (Worton 1989; Kie et al. 2010). Such techniques are however sensitive to the availability of location data (Seaman et al. 1999; Blundell et al. 2001), and the inclusion of individuals with few observations may have influenced the results of Stopher et al. (2012) through the under- or over-estimation of space use similarity. Thirdly, trait choice is likely to be important when drawing conclusions about the severity of the bias in heritability estimates as a result of not accounting for the space sharing of relatives. For example, Stopher et al. (2012) found large decreases in heritability estimates for two home range size (spring and rut) traits when accounting for the space sharing of related animals, leading them to conclude that heritability estimates can decrease dramatically when space sharing is accounted for. Given that they are spatial metrics, the home range size traits were very likely to have a spatially autocorrelated component. They were therefore useful to demonstrate that similarity in shared space can appear as similarity due to shared genes, providing an example of the potential severity of the bias when failing to account for space sharing by relatives. However, there is to our

knowledge little evidence to suggest that such traits have a heritable basis, particularly in mammals where home range size has been shown to vary with a wide variety of factors (van Beest et al. 2011b). The results for these traits are therefore unlikely to prove representative of the degree of bias in quantitative genetic parameters. There is a need to build on the study by Stopher et al. (2012), examining a wider range of traits, and focusing in particular on those that, based on previous research, are believed to be heritable. Indeed, although it is sensible to account for all suspected common environment effects when aiming to accurately estimate heritability, this may not always be possible given data limitations. Therefore studies are needed to better establish the likely extent of the bias in traits as a result of not accounting for such common environment effects.

Quantitative genetic analyses of wild populations are continuing to grow in popularity (Kruuk et al. 2008). This means it is essential to expand our understanding of potential biases in heritability estimates due to space sharing by related individuals, making use of the rapidly developing methodologies. The St. Kilda Soay sheep (*Ovis aries* Linnaeus, 1758) population is an ideal system for doing this. Firstly, females are philopatric, with relatedness increasing with home range proximity (Coltman et al. 2003). As a result, any phenotypic similarity between related females may be partially due to common environment effects resulting from space sharing. Secondly, there is spatial heterogeneity in the environment. Forage availability and quality varies markedly across the study area (Regan et al. 2016), with the highest quality grazing found in the previously cultivated meadows, and increasing density of low palatability species such as *Calluna vulgaris* as elevation increases (Coulson et al. 1999). Thirdly, because the population has been studied intensively for 30 years, we have sufficient data to quantify individual ranging behaviour and relatedness, making it possible to run animal models which include information on individual space use. Indeed, this population has been the focus of quantitative genetic analysis for many years,

providing an ideal platform for expanding on these modelling approaches. Furthermore, in contrast to many other long term studies of natural populations, a genomic relatedness matrix is available in place of a traditional pedigree. The use of this matrix has been recently shown to give more precise quantitative genetic estimates (Bérénos et al. 2014).

We aimed to understand how accounting for space sharing by related females affected our estimates of V_A or V_{MG} (maternal genetic effects) and h^2_T (the total heritability - accounting for additive and maternal genetic effects) or h^2 (the narrow-sense heritability) for five traits that are, based on previous research, believed to have a heritable basis (birth weight, birth date, lamb August weight, adult jaw length and adult metacarpal length). We predicted that individuals which were similar in their space use would be more similar in their phenotype (or the phenotype of their lambs), and that this would be particularly pronounced for birth weight, birth date and August weight, because these traits are closely tied to resource availability. Consequently, we also expected considerable bias in heritability estimates when space sharing was not accounted for. We provide only the second study to look at the effect of space sharing on estimates of heritability. Using improved methodologies we show that heritability estimates may be less affected by this source of common environment effect than previously thought.

4.3 Methods

4.3.1 Study population and data collection

The data used in this paper come from the Soay sheep population on the island of Hirta in the St. Kilda archipelago, Scotland (57°49° N 08°34° W). This population has been unmanaged since its introduction from the neighbouring island of Soay in 1932 (Clutton-Brock et al. 2004), and Hirta is now home to between 700 and 2300 Soay sheep, depending on variation in mortality between years. Sheep residing in

the Village Bay area of Hirta make up approximately one third of the total island population, and have been intensively studied since 1985 (Clutton-Brock et al. 2004).

The majority of lambs are ear-tagged within the first few days of life, making individuals uniquely identifiable. The mortality status of animals is tracked through regular censuses and mortality checks, with the census data also providing information on individual space use. Each August approximately two thirds of the Village Bay population are caught, at which time each individual is weighed. Because mortality is tracked closely, we are also able to take post mortem trait measurements from many animals, including jaw and metacarpal length. We selected three early life traits, birth weight, birth date and lamb August weight (all treated as a trait of the lamb), and two adult traits, female post mortem jaw length, and female post mortem metacarpal length. These traits were selected because they had previously been the focus of quantitative genetic study, and because of their potential link with resource availability. See Table 4.1 for heritability estimates for these traits from previous studies. For the adult traits, we incorporated information on the space sharing of all females with post mortem jaw and metacarpal length measurements. For the early life traits we used information on the space sharing of their mothers because at the point of measurement lambs have not developed their own home range. There are strong maternal genetic effects in all three early life traits (Wilson et al. 2005; Bérénos et al. 2014), and we were therefore interested in the change in this term when accounting for the space sharing of related mothers. There is no evidence for significant maternal genetic effects for either of the adult traits and therefore we did not estimate them in our analyses.

Table 4.1: Published estimates of the narrow-sense heritability (h^2), maternal genetic effect variance (m^2), and total heritability (h^2_T), when reported, for the five traits considered in this study. Hyphens represent cases where the parameter was not reported. Standard errors are provided in parentheses, where available. Note though that the fixed effects included in our models were similar (but not identical) to those included in models in these analyses. Because variance component ratios were calculated using the sum of the variance components as the denominator, reported heritabilities are conditional on fixed effects.

Trait	h^2	m^2	h^2_T	Reference
Birth weight	0.075 (0.045)	0.119 (0.045)	0.135(0.045)	Wilson et al. (2005)
(lamb)	0.160	0.250	-	Beraldi et al. (2007)
	0.069	0.284	-	Wilson et al. (2007)
	0.059 (0.017)	0.155 (0.033)	-	Bérénos et al. (2014)
Birth date	0.055 (0.036)	0.283 (0.051)	0.197 (0.038)	Wilson et al. (2005)
(lamb)	0.070	0.690		Beraldi et al. (2007)
August weight	0.047	0.017	-	Wilson et al. (2007)
(lamb)	0.104 (0.026)	0.103 (0.032)	-	Bérénos et al. (2014)
Jaw length	0.390	-	-	Beraldi et al. (2007)
(adult female)	0.594 (0.070)	-	-	Bérénos et al. (2014)
Metacarpal length	0.450	-	-	Beraldi et al. (2007)
(adult female)	0.556 (0.072)	-	-	Bérénos et al. (2014)

The analyses presented here were based on phenotypic records for individuals born between 1985 and 2012. Lambs were only included if their mother was dead to ensure that we were estimating lifetime space use for all animals. To prevent maternal rejections, we often delay weighing lambs until a few days after birth. As a result of early growth, the weight measurement will vary given the age at which they are caught. Because of this we restricted our birth weight analyses to individuals caught within five days of birth, and included capture age (in days) as a fixed effect in all birth weight models. We measured birth date as the number of days from 1 January, and August weight as the weight in kilograms of a lamb when it was caught in August. Jaw and metacarpal length measurements (in millimetres) were taken from bones that were collected and cleaned following mortality checks (see Beraldi et al. 2007 for more details), and in our analysis we only consider measurements taken from adult females (26 months or older) as skeletal growth is complete at this point (as indicated by an asymptote in the relationship between

age and both jaw and metacarpal length [CER, unpublished results]).

4.3.2 Space use

We opted for two methods of accounting for space sharing within the animal model framework used to estimate the genetic parameters, which are broadly comparable to those used in Stopher et al. (2012) (differences are described below). The first involves directly accounting for SAC in the response variable, whilst the second involves quantifying home range similarity for pairs of individuals and incorporating this as an additional matrix. We started by extracting spatial information for each individual. We census the 170 hectare Village Bay area 30 times per year, 10 times in each of the three routine trips to the island (April-May, July-August, October-November). During each census, three fixed routes are walked simultaneously, the identity of all individuals seen is noted and their grid reference is recorded to the nearest 100 metres. We extracted lifetime census observations for all females, excluding any individuals that had fewer than 49 census observations in total. 49 observations is the minimum number needed to give an asymptote in core home range area, thereby providing a reliable estimate of the home range (see Regan et al. 2016 for details). We transformed these observations onto a grid, so that the most south-westerly census observation (NF091980) became (0,0) and each step on the grid represented a distance of 100 metres.

We next estimated individual space use. In the case of the SAC model each individual had to be assigned a single spatial location. We therefore calculated average lifetime locations for each female, ensuring that this was estimated to the nearest 100 metres corresponding to the grid described above. From these grid references we can consider SAC in either the East-West (column) or South-North axis (row), or both simultaneously. To construct the home range similarity matrix necessary for the second method of accounting for space sharing in our animal models, we first estimated home ranges for each female. We estimated home ranges

(100% isopleth) using kernel density methods, calculating the smoothing parameter using the *ad hoc* method, within the package adehabitatHR (Calenge 2006). Because animals were assigned a grid reference to the nearest 100 metres during censuses, individuals frequently have numerous observations with identical grid references, and this can cause problems when estimating home ranges using kernel methods (Tufto et al. 1996). We therefore added a random number between -20 and 20 (representing a distance of up to 20 metres) to the X and Y coordinates for each record before estimating home ranges (see Moyes 2007 and Stopher et al. 2012). Powell (2000) suggests using core home ranges as they correspond to the area an animal uses most intensively, but here we were unable to do this because we could not construct a grid for home range estimation that was of a high enough resolution to give similarity metrics that scaled properly (i.e. between zero and one). We continued to consider only individuals with 49 or more observations, as doing so will still provide more reliable home range estimates, and similarity metrics. We then calculated home range overlap/similarity for all possible pairs of these females using Bhattacharyya's affinity (BA) (Bhattacharyya 1943; Fieberg and Kochanny 2005) in adehabitatHR (Calenge 2006). We used BA (see Fieberg and Kochanny 2005 for a summary of possible metrics) for two reasons. Firstly, because it uses three dimensional utilisation distributions (UDs), which describe both where a home range is located in space and the probability of re-sighting an animal at different points within this home range, it better captures how individuals use different parts of their home range (Fieberg and Kochanny 2005). Thus, this method provides more informative measures of similarity than metrics that consider only the spatial domain of the home ranges (Fieberg and Kochanny 2005). Secondly it scales from zero (no overlap) to one (identical UDs), making it comparable to genetic relatedness, which is important when trying to tease apart the contributions of these sources of similarity. This provided us with a matrix containing pairwise similarity metrics for 931 females that could be incorporated

into our models (see Fig. 4.1 for the distribution of BA values). In contrast to Stopher et al. (2012) we excluded individuals with insufficient census data in order to avoid potentially over- or under-estimating the bias caused by not accounting for space sharing.

4.3.3 Genomic relatedness matrix

When lambs are caught at birth they are sampled for genotyping. Individuals that are not caught at birth are sampled in August catches, by chemical immobilisation (darting, primarily of males during the rut), or post mortem. Genotypes at 37,037 informative autosomal single nucleotide polymorphism (SNP) markers on the Ovine SNP50 BeadChip (Illumina, for more information see Bérénos et al. 2014) are available for 5805 sheep spanning the period 1985-2012. The genomic relatedness between all pairs of SNP genotyped individuals was estimated in GCTA v1.04, which estimates the proportion of the genome identity-by-state between individuals (see Bérénos et al. 2014 for more details). This genomic relatedness matrix (GRM) was used in our animal models in place of the more traditional pedigree-derived additive relatedness matrix as it provides more accurate estimates of relatedness, leading to improved separation of direct and maternal genetic effects, and more precise estimates of quantitative genetic parameters (Bérénos et al. 2014).

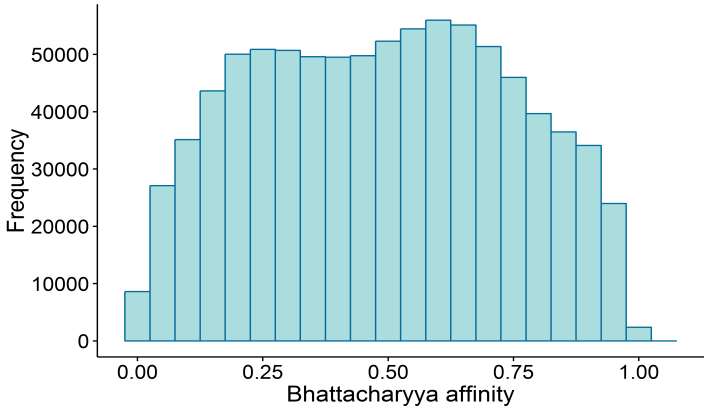

Figure 4.1: The distribution of Bhattacharyya affinity/home range overlap values contained in the full **S matrix**.

4.3.4 Analyses

All analyses were conducted in R version 3.1.3 (R Development Core Team 2008). We partitioned the phenotypic variance in each of the traits into genetic and environmental variance components using univariate animal models in ASReml-R (Butler et al. 2007). We included fixed effects to account for variation due to predictable effects such as sex and age. All models for early life traits included sex (two level factor), litter size (two level factor) and maternal age (linear and quadratic terms) as fixed effects. In addition, age at capture in days was included in models of birth weight (as a factor), and lamb August weight (as a covariate). For post mortem measures we only included a fixed effect of the age at death in months. After restricting on census observation number and removing individuals lacking the information needed to fit these fixed effects, we had birth weights for 1772 lambs (from 380 females), birth dates for 2124 lambs (404 females), August weights for 1043 lambs (334 females), and 300 and 286 females for jaw and metacarpal length analyses respectively.

We then added random effects sequentially. Firstly, we included a random effect of individual identity linked with the GRM to estimate the additive genetic effect

(V_A, or the additive influence of genes carried by the individual in which the trait was measured). Secondly, we included a random effect of the year of birth, to partition the variance attributable to variation in the environment in the first year of life (V_{YoB}), followed by the identity of the individual's mother in order to estimate maternal effects (assuming that they are entirely environmental) (V_{ME}). Thirdly, in the case of the early life traits, we also fitted a maternal genetic effect (V_{MG}) to decompose the maternal effect variance into maternal permanent environment and maternal genetic components. This is important, as in the case of the early life traits we expect any bias caused by not accounting for space sharing by related females to be found in this maternal genetic effect component. Finally, we estimated the direct-maternal genetic covariance (COV_{am}) to enable the calculation of the total heritability.

We then accounted for space sharing in the following ways. Firstly, to account for spatial dependence in the response variable, we incorporated average lifetime locations by fitting column and row as additional random effects, with an isotropic exponential covariance structure, equivalent to a continuous AR1 times AR1 process (Gilmour et al. 2009). This allows us to account for spatial autocorrelation between the residuals by dividing the residual error variance into spatially dependent and spatially independent residuals. It makes it possible to use an incomplete spatial array (where some intersections are not occupied by an individual) by including column and row as random effects (Dutkowski et al. 2002), whilst also facilitating the examination of autocorrelation in row and column directions separately (Dutkowski et al. 2002). In models with the SAC process, we estimated both the variance explained by column and row ($V_{Column\ and\ row}$), and the strength of the autocorrelation (r). Secondly, we included information on home range similarity by fitting either individual identity (jaw and metacarpal length) or maternal identity (birth weight, birth date and lamb August weight) as an additional random effect, but this time linking it with our spatial similarity matrix

(referred to subsequently as the '**S matrix**', with the corresponding variance component referred to as $V_{Smatrix}$).

The total phenotypic variance (denoted as Sum V in Table 4.2) was estimated as the sum of all variance components, and the variance explained by each of the variance components was calculated as the ratio of the relevant component to the total phenotypic variance. The direct additive-maternal genetic correlation (r_{am}) was calculated as $COV_{am}/\sqrt{V_A.V_{MG}}$. To account for maternal genetic effects and the direct additive-maternal genetic covariance when estimating heritability, we calculated the total heritability (h^2_T) as (V_A + 1.5COV_{am} + 0.5V_{MG})/Sum V (sensu Willham (1972), and following (Wilson et al. 2005)). We used likelihood ratio tests to assess the significance of random effects, assuming a χ^2 distribution with degrees of freedom equal to the number of additional parameters. However, because variance components cannot be smaller than zero (meaning the boundary condition is violated) the use of one degree of freedom can be overly conservative (Visscher 2006). To gauge model credibility, we summed the variance component estimates from each model, with large changes in this total variance indicating potential problems with model performance, and that variance component estimates should be interpreted with some caution. In the Results, attention is drawn to models where this was the case, with the interpretation adjusted accordingly. For example code please see Appendix B.

4.4 Results

Early life traits

We found evidence for strong maternal effects on all three early life traits, and models including maternal genetic effects (alongside maternal permanent environment effects and no spatial structure) performed significantly better than those estimating purely environmental maternal effects with no spatial structure

(Birth weight - $\chi^2_{(df=1)}$=21.05, P< 0.001; Birth date - $\chi^2_{(df=1)}$=22.82, P< 0.001; August weight - $\chi^2_{(df=1)}$=14.12, P< 0.001). In fact, the estimate of the maternal genetic effect variance was consistently greater than that of the direct heritability for all three early life traits (Table 4.2). We did not however find any evidence for a significant direct-maternal genetic covariance for any of the three early life traits (Birth weight - $\chi^2_{(df=1)}$=0.001, P=0.97; Birth date - $\chi^2_{(df=1)}$=0.073, P=0.79; August weight - $\chi^2_{(df=1)}$=1.90, P=0.17).

We did however find some differences between these traits in the proportion of variance explained by the spatial term. For birth weight, inclusion of the **S matrix** significantly improved model fit ($\chi^2_{(df=1)}$=13.32, P< 0.001), and the term explained 5.6% of the variance (Table 4.2). Its incorporation resulted in small reductions in the estimates of V_{MG} (1.5% (from 16.9% to 15.4%), see Table 4.2) and V_{ME} (1.1% (from 2.9% to 1.8%), see Table 4.2), and therefore a negligible reduction in h^2_T (1.4% (from 9.4% to 8.0%), see Table 4.2). We found a similar trend when using the SAC models, again with a significant improvement in model fit when the spatial terms were added ($\chi^2_{(df=3)}$=10.56, P=0.014). The autocorrelation parameter indicated positive SAC (r=0.80), but column and row random effects only accounted for 3.6% of the variance and were associated with only a 2.3% reduction (from 16.9 to 14.6%) in the estimate of V_{MG}. The large standard errors, particularly around the estimate of the spatial variance component (Table 4.2), indicate that the model had some difficulty in estimating them, and lends credence to the idea that spatial variation in the environment does not generate substantial variation in lamb birth weight.

Including the **S matrix** also significantly improved model fit in the case of birth date ($\chi^2_{(df=1)}$=9.38, P=0.002). The spatial term accounted for 6.0% of the variance in birth date, and the change in the estimate of V_{MG} induced by not accounting for space sharing was higher than for birth weight, though still small, declining by 6.6% (from 25.5% to 18.9%) (Table 4.2, Fig. 4.2). The reduction in the maternal

genetic effect estimate translated into a 3.4% decrease (from 17.1% to 13.7%) in the estimate of h^2_T (Table 4.2). When it came to the SAC model for birth date, we found evidence for a marginally significant improvement in model fit upon including column and row effects $\chi^2_{(df=3)}$=7.94, P=0.047), but there was substantial variance inflation upon incorporation of SAC, with the total variance explained increasing from 54.01 to 40935.84 (raw observed variance=48.971). Small changes in the variance explained are not of particular concern, but large changes may indicate that the model has produced poor parameter estimates (Stopher et al. 2012). This was associated with the spatial variance component becoming singular (Table 4.2), which prevented convergence. This suggests that there is too little spatial variance in the data to enable the estimation of the spatial parameters.

We also found that the **S matrix** significantly improved model fit when added to the model of August weight ($\chi^2_{(df=1)}$=10.12, P=0.001), but compared with the previous two traits, the spatial term accounted for a much larger proportion of the total variance (17.8%, see Table 4.2 and Fig. 4.2). Despite this, the change in h^2_T caused by not accounting for the space sharing of females was on par with birth weight and birth date, with the estimate of V_{MG} reduced by only 4.9% (from 13.5% to 8.6%), and h^2_T reduced by 3.9% (Table 4.2). The results from the SAC model for August weight were similar to those from the birth date models. The model estimated a very large autocorrelation coefficient of 0.999 (Table 4.2), indicating very strong positive SAC in lamb August weight. However, the model failed to estimate the spatial variance component, with the estimate for this component increasing in size with each iteration before going singular (Table 4.2), and therefore preventing convergence. As in the case of birth date, this pattern may indicate that there is too little spatial variance in the data to enable the autocorrelation parameter to be estimated.

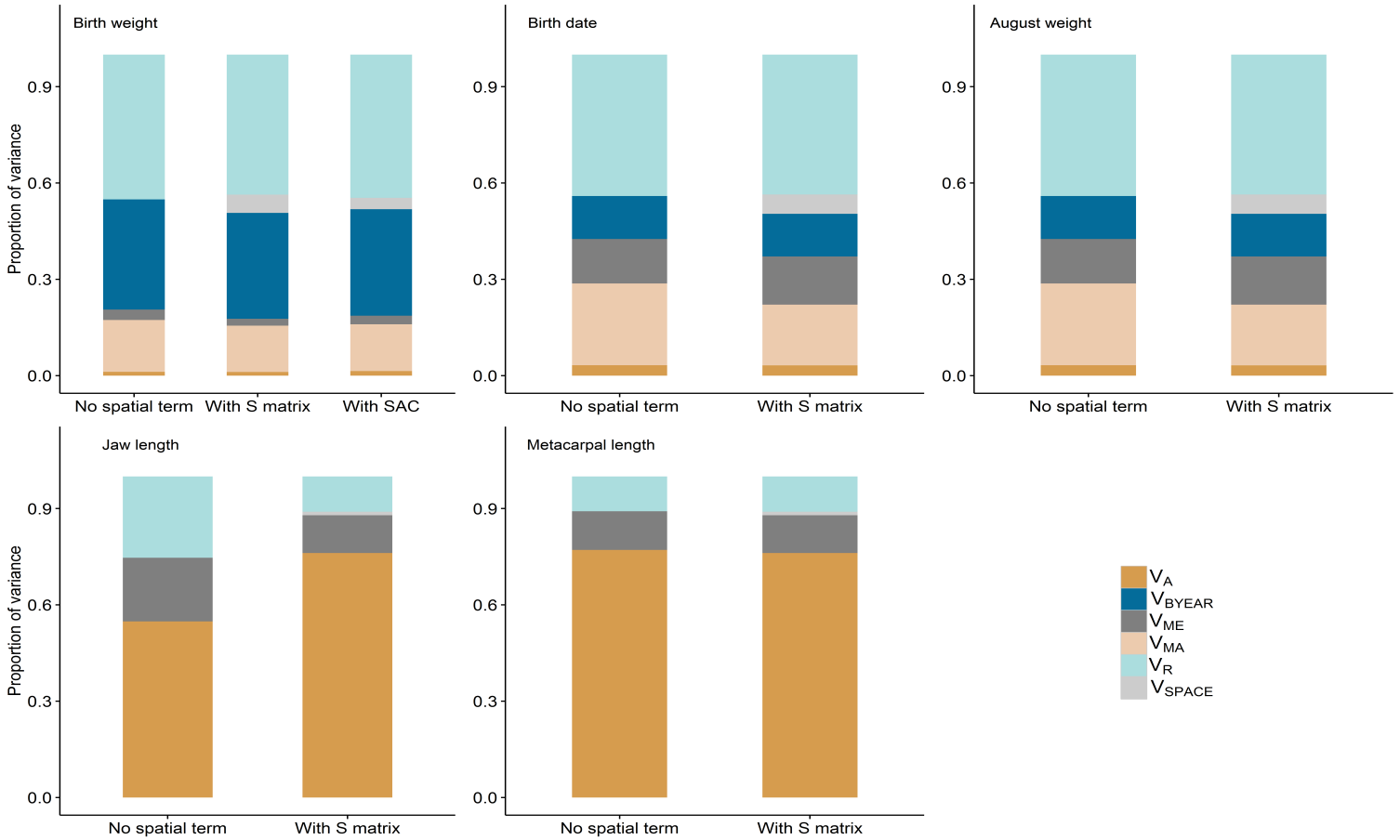

Figure 4.2: The proportions of variance explained by different random effects in animal models for three early life, and two adult traits measured in St. Kilda Soay sheep. For all traits we present the results for models containing no spatial term, and with the home range similarity matrix (or '**S matrix**'), however we only present the results from spatial autocorrelation models ('With SAC') for the traits where SAC models converged.

Adult traits

As expected from previous analyses, our estimates of h^2 (the ratio of V_A to the total trait variance) were much larger for jaw length and metacarpal length, than for the three early life traits (see Table 4.2), with only small amounts of variance attributable to birth year and maternal effects (see Table 4.2 and Fig. 4.2). We found a marginally significant improvement in model fit when adding the **S matrix** in the case of jaw length ($\chi^2_{(df=1)}$=3.96, P=0.046), with the term accounting for 8.2% of the variance in the trait (Table 4.2 and Fig. 4.2). The incorporation of the **S matrix** did result in a reduction in the estimate of h^2, though this was still relatively small at 6.8% (from 54.9% to 48.0%) (Table 4.2). For jaw length, the incorporation of SAC did not significantly improve model fit ($\chi^2_{(df=2)}$=1.87, P=0.599), explaining only 3.0% of the variance and resulting in only a 2.8% decrease (from 54.9% to 52.1%) in the estimate of h^2 (Table 4.2). In contrast to jaw length, adding the **S matrix** to models of metacarpal length did not improve model fit ($\chi^2_{(df=1)}$=0.11, P=0.74), and the term accounted for only 1.1% of the variance (Table 4.2 and Fig. 4.2). As a result we saw only a 1% reduction (from 77.1% to 76.1%) in the estimate of h^2 (Table 4.2). The SAC models echoed this result, as we saw no improvement in model fit upon the inclusion of SAC ($\chi^2_{(df=1)}$=-21.81, P>0.99), with it accounting for only 4.2% of the variance in the trait (Table 4.2 and Fig. 4.2). In addition, the very small autocorrelation parameter (that eventually went singular, see Table 4.2), suggests there is little evidence that animals which are similar in their space use are more similar in their metacarpal lengths than animals which range in very different parts of the study area. Please see Table 4.3 for fixed effects coefficients for each trait.

Table 4.2: Variance component estimates and their associated ratios for models including no spatial term, with the **S matrix** (containing home range similarity metrics), or with spatial autocorrelation, for three early life, and two adult traits measured in St. Kilda Soay sheep. Reported are the additive genetic variance (V_A), birth year variance (V_{YoB}), maternal permanent environment variance (V_{ME}), maternal genetic variance (V_{MG}), **S matrix** variance ($V_{Smatrix}$), SAC variance ($V_{Column\ and\ row}$), the total variance (Sum V), the autocorrelation coefficient (Autocorrelation (r)), the direct additive-maternal genetic covariance (COV_{am}) and correlation (r_{am}), and the total heritability (h^2_T, accounting for maternal genetic effects and the direct additive-maternal genetic covariance). We provide both the raw variance component/correlation estimates ('Est'), and the proportion of the total variance explained by the term in the case of variance components ('Prop'). Standard errors are provided in parentheses, and singular parameters (with 'NA' standard errors)/parameters that were fixed at the boundary are italicised.

	No spatial term		With S matrix		With SAC	
	Est	Prop	Est	Prop	Est	Prop
Birth weight						
V_A	0.003 (0.004)	0.014 (0.018)	0.003 (0.004)	0.014 (0.017)	0.003 (0.004)	0.014 (0.017)
V_{YoB}	0.081 (0.024)	0.336 (0.069)	0.081 (0.025)	0.324 (0.069)	0.081 (0.024)	0.332 (0.070)
V_{ME}	0.007 (0.007)	0.029 (0.030)	0.004 (0.007)	0.018 (0.027)	0.007 (0.007)	0.027 (0.028)
V_{MG}	0.041 (0.011)	0.169 (0.047)	0.038 (0.011)	0.154 (0.043)	0.035 (0.011)	0.146 (0.043)
$V_{Smatrix}$			0.014 (0.010)	0.056 (0.040)		
$V_{Column\ and\ row}$					0.009 (0.010)	0.036 (0.040)
$V_{Residual}$	0.108 (0.005)	0.451 (0.053)	0.108 (0.005)	0.436(0.052)	0.108 (0.005)	0.446 (0.055)
Sum V	0.240		0.249		0.243	
Autocorrelation (r)					0.778 (0.316)	
COV_{am}	$-8.830\times e^{-4}$ (0.006)		-0.002 (0.005)		$-1.306\times e^{-3}$ (0.005)	
r_{am}	-0.075 (0.445)		-0.158 (0.427)		-0.119 (0.451)	
h^2_T	0.094 (0.030)		0.080 (0.027)		0.079 (0.028)	
Birth date						
V_A	1.740 (1.077)	0.032 (0.020)	1.759 (1.085)	0.032 (0.020)	1.700 (1.080)	$4.153\times e^{-5}$ ($2.762\times e^{-5}$)
V_{YoB}	7.245 (2.208)	0.134 (0.036)	7.282 (2.220)	0.133 (0.036)	7.358 (2.244)	$1.797\times e^{-4}$ ($5.558\times e^{-5}$)
V_{ME}	7.478 (2.608)	0.138 (0.049)	8.231 (2.559)	0.150 (0.048)	8.404 (2.588)	$2.053\times e^{-4}$ ($6.463\times e^{-5}$)
V_{MG}	13.757 (3.810)	0.255 (0.063)	10.366 (3.503)	0.189 (0.060)	10.887 (3.538)	$2.660\times e^{-4}$ ($8.781\times e^{-5}$)
$V_{Smatrix}$			3.314 (2.776)	0.060 (0.048)		
$V_{Column\ and\ row}$					*40883.58 (1898.87)*	0.999 (0.0001)
$V_{Residual}$	23.793 (1.105)	0.441 (0.035)	23.912 (1.112)	0.436 (0.038)	23.915 (1.111)	$5.842\times e^{-4}$ ($5.930\times e^{-8}$)
Sum V	54.014		54.864		40935.84	

Autocorrelation (r)					1.000	
					(2.904×e^{-6})	
COV_{am}	0.455 (1.539)		0.417 (1.462)		0.185 (1.469)	
r_{am}	0.093 (0.327)		0.098 (0.357)		0.043 (0.348)	
h^2_T	0.171 (0.042)		0.137 (0.041)		1.813×e^{-4}	
					(5.870×e^{-5})	
August weight						
V_A	0.198 (0.192)	0.036 (0.035)	0.170 (0.189)	0.029 (0.032)	0.163 (0.186)	1.612×e^{-5}
						(1.921×e^{-5})
V_{YoB}	2.129 (0.658)	0.391 (0.075)	1.670 (0.527)	0.287 (0.074)	1.970 (0.606)	1.945×e^{-4}
						(6.178×e^{-5})
V_{ME}	0.021 (0.191)	0.004 (0.035)	0.043 (0.176)	0.007 (0.030)	0.053 (0.180)	.284×e^{-6}
						(1.788×e^{-5})
V_{MG}	0.737 (0.291)	0.135 (0.052)	0.498 (0.253)	0.086 (0.044)	0.532 (0.260)	5.255×e^{-5}
						(2.630×e^{-5})
$V_{Smatrix}$			1.032 (0.629)	0.178 (0.093)		
$V_{Column\ and\ row}$					*10117.65*	*0.999*
					(765.167)	*(7.399×e^{-5})*
$V_{Residual}$	2.359 (0.182)	0.433 (0.065)	2.397 (0.183)	0.413 (0.064)	2.405 (0.182)	2.376×e^{-4}
						(1.759×e^{-8})
Sum V	5.445		5.810		10122.77	
Autocorrelation (r)					1.000	
					(6.989×e^{-6})	
COV_{am}	0.244 (0.169)		0.222 (0.158)		0.226 (0.157)	
r_{am}	0.638 (0.658)		0.764 (0.871)		0.767 (0.864)	
h^2_T	0.164 (0.046)		0.125 (0.041)		7.589×e^{-5}	
					(2.592×e^{-5})	
Jaw length						
V_A	9.974 (2.834)	0.549 (0.129)	9.045 (2.726)	0.480 (0.129)	9.375(2.768)	0.521 (0.131)
V_{YoB}	*4.659×e^{-7}*	*2.562×e^{-8}*	*5.177×e^{-7}*	*2.747×e^{-8}*	*3.327×e^{-3}*	*1.848×e^{-4}*
	(2.332×e^{-7})	*(1.376×e^{-8})*	*(2.324×e^{-8})*	*(1.336×e^{-8})*	*(7.729×e^{-3})*	*(4.305×e^{-4})*
V_{ME}	3.603 (1.761)	0.198 (0.092)	3.137 (1.724)	0.166 (0.089)	2.986 (1.752)	0.166 (0.094)
$V_{Smatrix}$			1.548 (1.493)	0.082 (0.074)		
$V_{Column\ and\ row}$					0.546 (0.846)	0.030 (0.046)
$V_{Residual}$	4.604 (2.305)	0.253 (0.136)	5.116 (2.297)	0.271 (0.132)	5.092 (2.330)	0.283 (0.140)
Sum V	18.180		18.846		18.003	
Autocorrelation (r)					0.630 (0.840)	
Metacarpal length						
V_A	10.340 (2.741)	0.771 (0.110)	13.306 (2.744)	0.761 (0.114)	9.683 (1.498)	0.414 (0.065)
V_{YoB}	*3.008×e^{-7}*	*1.731×e^{-8}*	*1.946×e^{-7}*	*1.113×e^{-8}*	*0.004(0.374)*	*1.762×e^{-4}*

	(3.138×e^{-7})	*(1.878×e^{-8})*	*(1.987×e^{-7})*	*(1.182×e^{-8})*		*(0.016)*
V_{ME}	2.094 (1.402)	0.121 (0.079)	2.054 (1.397)	0.118 (0.078)	2.417 (1.534)	0.103 (0.067)
$V_{Smatrix}$			0.020 (0.068)	0.011 (0.039)		
$V_{Column\ and\ row}$					0.973 (0.842)	0.042 (0.036)
$V_{Residual}$	1.885 (1.966)	0.108 (0.118)	1.923 (1.963)	0.110 (0.117)	10.301 (2.435)	0.441 (0.067)
Sum V	17.379		17.479		23.379	
Autocorrelation (r)					*2.148×e^{-69}(NA)*	

Table 4.3: Coefficients and standard errors of fixed effects for each of the five traits featured in this study. For early life traits, values are taken from a model including only the fixed effects shown in the table, and additive genetic, birth year, maternal permanent environment, maternal genetic random effects and a direct-maternal genetic covariance. For the adult skeletal traits, values are taken from a model including only the fixed effects below, and additive genetic, birth year, and maternal permanent environment random effects.

Trait	Fixed effect	Level	Coefficient	Standard Error
Birth weight	Litter size	Singleton	0.000	NA
	Litter size	Twin	-0.795	0.023
	Sex	Female	0.000	NA
	Sex	Male	0.119	0.017
	Maternal age		0.438	0.014
	Maternal age^2		-0.031	0.001
	Capture age	Day zero	0.000	NA
	Capture age	Day one	0.245	0.042
	Capture age	Day two	0.397	0.041
	Capture age	Day three	0.481	0.044
	Capture age	Day four	0.518	0.049
	Capture age	Day five	0.552	0.057
Birth date	Litter size	Singleton	0.000	NA
	Litter size	Twin	0.003	0.330
	Sex	Female	0.000	NA
	Sex	Male	0.015	0.024
	Maternal age		-0.016	0.190
	Maternal age^2		0.0001	0.016
August weight	Litter size	Singleton	0.000	NA
	Litter size	Twin	-3.441	0.145
	Sex	Female	0.000	NA
	Sex	Male	1.521	0.107
	Maternal age		1.742	0.093
	Maternal age^2		-0.134	0.008
	Capture age		0.066	0.008
Jaw length	Age at death		0.059	0.006
Metacarpal length	Age at death		0.009	0.006

4.5 Discussion

As predicted, we found that increased similarity in female space use was associated with greater phenotypic similarity. This was most evident for the early life traits, with females that had more similar home ranges having lambs that were more similar in their birth weights, birth dates, and August weights. Despite this, and contrary to our expectation, the increase in the (total) heritability estimates caused by not accounting for home range similarity was small, ranging from 1.4% (from 8.0% to 9.4%) to 6.8% (from 48.0% to 54.9%) depending on the trait considered.

Home range similarity generally explained a significant amount of variation in the traits considered, which aligns with previous research on the St. Kilda Soay sheep. Environmental components such as forage availability and quality vary markedly across the study area (Coulson et al. 1999; Regan et al. 2016). Such spatial variation in grazing quality means that sheep inhabiting different regions of the study area have access to food resources of differing quality, something that has been posited to lead to the variation in survival, recruitment and dispersal that we see across hefts (a heft being a group of individuals, regardless of sex or age, that use the same resources in space) (Coulson et al. 1999). Recent work has supported this idea, showing that variation in home range quality (measured as the home range percentage cover of *Holcus lanatus*, a key component of the *Holcus-Agrostis* plant community known to be highly palatable to the sheep (Crawley et al. 2004), is associated with variation in both male and female lifetime reproductive success (Regan et al. 2016). Given the heterogeneity in grazing quality across the study area, and the fact that females exhibit high fidelity to their natal heft (Coltman et al. 2003), it would follow that neighbouring animals are more phenotypically similar, particularly in traits such as birth weight and August weight. This is because these traits are likely to be strongly determined by the quantity and quality of food resources available to the mother during gestation and lactation

(Oftedal 1984). Though the **S matrix** improved model fit for all traits other than metacarpal length the proportion of variance explained by the spatial term was generally smaller than expected, particularly in the case of birth weight. There is one likely explanation for this result. Hirta's Soay sheep do not conform to the ideal free distribution (Jones 2006). Not only is *Holcus-Agrostis* grassland used by a greater proportion of the population than would be predicted from its availability, but its occupancy actually increases with sheep density (Jones 2006). This likely means that changes in population density compensate to some degree for the variation in grazing quality.

There are two conditions that need to be met for heritability estimates to be biased by disregarding the space use of animals. Firstly, relatives must be clustered in space as it is under this condition that phenotypic similarity due to shared genes may be confounded with similarity due to space sharing. The reason for this potential bias becomes clear when we consider variance partitioning methods. Assuming genetic and environment effects combine additively to determine phenotype, such that:

$$V_{\mathrm{P}} = V_{\mathrm{G}} + V_{\mathrm{E}}$$

It is apparent that such a model is only valid when there is no genotype-environment covariance. To meet this assumption any sources of correlation (i.e. common environment effects) must be accounted for elsewhere in the model. Social structure and natal philopatry are common in wild vertebrate populations, having been found in birds (Greenwood 1980), mammals (Greenwood 1980), reptiles (Sheridan et al. 2010), amphibians (Helfer et al. 2012), and fish (Mourier and Planes 2013). As a result, the condition that relatives be clustered in space is likely to be satisfied for many natural populations. The degree of bias induced by failing to account for space sharing by relatives may however vary given the degree to which relatives are clustered in space, and the time scale over which

the clustering is maintained. Complications may arise when considering migratory species, given that trait variation may be associated with conditions at either the wintering or breeding ground, or even both (Norris et al. 2004; Ockendon et al. 2013).

The second condition required for bias to occur is that the environment must be spatially heterogeneous, as it is this heterogeneity that will mean relatives are more likely to experience similar fine-scale environmental variation, and therefore appear more similar, than non-relatives. Again, this condition is likely to be satisfied in studies of natural populations, but the spatial scale, and pattern of this environmental heterogeneity is likely to be important, because it will influence the degree of environmental similarity experienced by relatives, compared to non-relatives. Though not a necessary condition for bias, trait choice should be carefully considered when drawing conclusions about the effect of including space sharing on heritability estimates. Accurately estimating heritability in quantitative genetic studies will necessitate the accounting of potential sources of common environment effects, such as space sharing by relatives. We therefore advocate for space sharing to be included, where the above conditions are met and where possible, into quantitative genetic analyses. However, it may be fruitful to focus on traits that, based on previous research, are believed to be heritable. Given the relatively limited knowledge surrounding the extent of the bias caused by space sharing it may be most economical to focus on the wide variety of traits for which substantial heritability is apparent in the literature. Furthermore, the degree of bias in heritability estimates as a result of failing to account for space sharing by related animals will be closely related to the degree of heritability in the trait. Despite fulfilling the above conditions and using traits believed to be heritable, we found no evidence of substantial bias in heritability estimates for any of the five traits studied. This suggests that these conditions alone are necessary but not sufficient to generate substantial bias in heritability estimates. Improving our understanding

of philopatry in the St. Kilda Soay sheep will enable us to better put our findings into perspective. For example, we do not currently know how the associations between related individuals change over time. It is likely that these associations are not static, given that we know that female ranging behaviour changes with age in Soay sheep (Hayward et al. 2015). Similarly, it may be that dispersal varies across the study area, or between years, because of variation in habitat quality, resource availability or population density. Indeed, dispersal is known to vary with environmental conditions in a wide range of species (Matthysen 2005).

Our results suggest that although spatial effects can cause upward bias of heritability estimates, this is not always the case. This conclusion contrasts to those drawn in the two previous studies that have examined the change in heritability estimates when accounting for space sharing. In both cases they suggested that the bias was likely to be considerable, potentially up to 25% and 43%, respectively (Van Der Jeugd and McCleery 2002; Stopher et al. 2012). Our estimates are likely to be more robust for the following reasons. Firstly, by using the animal model rather than parent-offspring regression (as used in Van Der Jeugd and McCleery (2002)), and a genomic relatedness matrix (GRM) instead of a traditional pedigree, the genetic parameter estimates are likely to be more precise (Kruuk 2004; Akesson et al. 2008; Bérénos et al. 2014)(though note that animal models were used in Stopher et al. 2012). Secondly, when it came to the **S matrix** approach, we only estimated home ranges, and calculated similarity metrics, for females with at least 49 census observations. Kernel density methods are sensitive to the availability of location data (Seaman et al. 1999; Blundell et al. 2001), and we wanted to ensure that our spatial estimates were not influenced by poor home range estimates for individuals with few data, and assumptions of zero overlap for individuals with no data. It is likely that in other studies spatial data will be more limiting than in our case. The number of observations necessary to accurately estimate home ranges will however vary between systems and with the method in which the spatial data

were collected. It will therefore be important to calculate the likely number of observations needed for accurate home range estimation on a case-by-case basis. Where smaller spatial datasets are available it may be possible to run the analyses with subsets of individuals that vary in their number of observations in order to understand how this influences results. In addition, it may be possible to use tools such as Bayesian kernel density estimators (Zhang et al. 2006) to appropriately account for the uncertainty surrounding home range estimates when deriving overlap metrics. Fourth, and finally, by choosing traits that based on previous research were believed to be heritable we hope our results will provide a useful benchmark for further studies of this kind. As mentioned above, trait choice is likely to be important when drawing conclusions about the expected change in heritability estimates upon accounting for the space sharing of relatives. For example, the large change in the estimated heritability for home range size traits upon including space sharing that was uncovered by Stopher et al. (2012) suggested that the bias in heritability estimates is likely to be substantial. These traits are very likely to be spatially variable given their close link with food availability (Tufto et al. 1996; Eide et al. 2004). This made them ideal for illustrating the bias that could be expected under a worse-case scenario but such traits are unlikely to yield representative estimates of the degree of bias in quantitative genetic parameters because there is, to our knowledge, little evidence to suggest that they have a heritable basis, particularly in mammals. This suggestion is supported by the fact that the results from **S matrix** models of birth weight were largely comparable between our study and that of Stopher et al. (2012). Both the proportion of variance explained by the spatial term (5.6% in our analysis, and 5.9% in Stopher et al. (2012)), and the change in the estimate of h^2 when not accounting for shared space (1.4% (from 9.4% to 8.0%) in our analysis, and 2.6% (from 28.2% to 25.6%) in Stopher et al. (2012)) were of similar magnitude.

The results from SAC models for birth weight reported here were less similar to

those of Stopher et al. (2012). In our analysis, the results from the two methods were generally comparable, but in the analysis by Stopher et al. (2012), incorporation of the SAC process resulted in the proportion of variance explained by the spatial term increasing to 19.5% (from 5.9% when using the **S matrix**), and an absolute change in the estimate of h^2 of 14.4%. As Stopher et al. (2012) suggest, their results may indicate that different spatial processes are at work, but there was some indication that their SAC model could not estimate the autocorrelation coefficient, given that it was fixed at the boundary. Furthermore, the standard error around the variance component estimate for the spatial term was very large (estimate=0.336, standard error=0.700), suggesting that there may be little spatial variation in birth weight. Consequently, our results appear to be more closely aligned with those of Stopher et al. (2012) than it may at first seem.

In light of this work we make some recommendations for future studies aiming to account for space sharing by relatives when running quantitative genetic analyses. In some cases our SAC models poorly estimated the autocorrelation parameter and the variance explained by SAC. Though these models can indicate whether there is spatial dependence in a trait, it is difficult to put weight on the estimates of the spatial variance component, and therefore on the change in the estimated heritability. The problems we and Stopher et al. (2012) have identified with the SAC models is perhaps unsurprising, given that they were developed for the analysis of agricultural variety trials (Cullis and Gleeson 1991). The data from such trials differ considerably to those from long-term studies of animal populations, and this has the potential to influence the suitability of SAC approaches. For example, crop and forestry trials deal with non-mobile organisms, that have single spatial locations. We can assign animals single locations, making it possible to run SAC models, but this may reduce our ability to detect a spatial signal, having averaged over detailed information on individual space use. Furthermore, by averaging over each individual's location data multiple animals

often have the same average location (at least over the spatial scale we were able to work at), despite the fact that they do vary in their space use. This too could make it difficult to detect a spatial trend. Finally, we can often record the locations of plants at a much higher precision than that of wild animals. For example, in the case of the Soay sheep, census data are only recorded to the nearest 100 metres. Therefore, when it comes to studies of wild animals, there is often a much coarser grid over which to run these analyses. This is likely to be one of the key reasons for the poor estimation of the autocorrelation parameter and/or the spatial variance component in our SAC models. As a result, we agree with Stopher et al. (2012) in advocating the **S matrix** approach. Not only is it relatively straightforward to fit, but it is arguably the best available way of including information on space use similarity in animal models. This is because it uses similarity metrics that are based on three dimensional utilisation distributions, which tell us not only where a home range is located, but actually to what degree animals use different parts of this home range (Worton 1989). One potential limitation of the **S matrix** approach is that, by capturing information on home range overlap/similarity, it can say nothing about individuals that live adjacent to each other but have non-overlapping utilisation distributions according to Bhattacharyya's Affinity. Though it is unlikely that two animals could live at close quarters without overlapping at all in their distributions, it may be inappropriate to leave SAC models behind altogether, because they provide a means to capture this information.

Though our work shows that quantitative geneticists may have confidence in their heritability estimates, there is some way to go before we can make informed predictions about the degree of bias in heritability estimates when we cannot, or do not account for spatially derived similarity. As a result, a key avenue for future research is in understanding whether the degree of bias varies between species, given the huge variation in dispersal patterns in nature. This will make it possible to predict the need for spatial components in quantitative genetic models in the

future. It is also important to consider precisely what aspect of the environment is varying spatially when conducting these analyses. In our study, we were generally concerned with capturing the effect of variation in resource availability, with such variation likely to impact traits associated with growth. In other studies, however, the focus may be on spatial variation in predation risk due to variation in substrate colour or vegetation structure, or even spatial variation in the social environment due to differences in, for example, density. This focus will dictate which traits are of most interest, or where bias is of greatest concern.

There are two other exciting avenues for research that we wish to draw attention to. Firstly, though we accounted for phenotypic similarity caused by individuals being born in the same year, the current models lack information regarding temporal variation in the environment after the year of birth and temporal changes in space use itself. Currently, these models treat individuals with a given home range overlap, or neighbouring average lifetime locations, equivalently, whether they were alive at the same time or their lives never overlapped. This assumption of equality regardless of temporal overlap is probably over-simplifying, and penalising the similarity metric for individuals whose lives did not overlap might result in smaller changes in heritability estimates upon including space sharing. Ranging behaviour itself may vary temporally, and therefore it may be necessary to consider the temporal scale at which space sharing is quantified more carefully. For example, early life traits may be more dependent on environmental variation at a temporal scale below that of the lifetime, because the body mass/condition of adult females is likely determined at this scale. Indeed, a number of mammalian studies have shown variation in adult body mass/condition in relation to temporal variation in the environment (Clutton-Brock and Albon 1983; Toïgo et al. 2006). It may therefore be preferable to analyse such traits using an **S matrix** constructed at a more appropriate temporal scale. The suitability of this approach will, however, depend on data availability, as animal models are

necessarily data hungry. Secondly, though perhaps unlikely in mammals, traits associated with ranging behaviour may have a genetic basis. Indeed there have now been a number of quantitative genetic studies focusing on traits associated with ranging behaviour and dispersal (Waser and Thomas Jones 1989; Hansson et al. 2003; Doligez et al. 2009; Charmantier et al. 2011), the majority of which have focused on birds. If there is a genetic element to space use itself, then it is possible that by accounting for space sharing of related individuals heritabilities may be underestimated (Stopher et al. 2012).

In conclusion, we find that despite significant spatial variation in a variety of heritable traits there were only small changes in heritability estimates when we failed to account for the fact that related female Soay sheep share space because of natal philopatry. This suggests that heritability estimates from prior quantitative genetic studies of this population are likely to be reliable. Though this is reassuring further research will be needed before we can be confident of the generality of these results. We hope that this work will encourage researchers to include spatial processes in their animal models when their data fulfil the conditions under which we would expect bias in heritability estimates by not accounting for space sharing. Not only that, we hope that they will publish their results, even when heritability estimates are largely unchanged, so that we can better predict when bias may be of particular concern.

Chapter 5

Is the maternal genetic effect on lamb growth mediated by differences in maternal care?

5.1 Abstract

The care provided by parents varies substantially between species, and between individuals of the same species. Much research has focused on the role of ecological conditions in generating variation in parental care, but such variation may also arise due to intrinsic genetic differences between individuals. Although the development of the quantitative genetic animal model has made it possible to estimate genetic components of phenotypic (co) variance in natural population, little remains known about the genetic basis of parental care in such systems. This is largely because the behavioural data necessary are not available for the populations amenable to quantitative genetic research. Here, we explore an indirect approach for examining the role of genetic differences between individuals in generating variation in parental care. We used the animal model to predict maternal breeding values for lamb growth, and used these predictions to select females for field observation, where both maternal and lamb behaviours were recorded. We found evidence that predicted maternal breeding value was associated with suckling success, indicating that lambs born to mothers whose genotype was associated with faster lamb growth experienced fewer unsuccessful suckling bouts. There was also evidence to suggest that a mother's predicted breeding value was also associated with the amount of time a lamb spent resting during each focal observation. Though our work is unable to explicitly estimate the genetic basis of the specific behavioural traits involved, it does suggest that variation in behaviour over the maternal care period may be involved in the pathway that generates maternal genetic effects on lamb growth in Soay sheep. Further research will be necessary to uncover the specific maternal traits underlying the patterns we observed, but the approach put forward here may extend the ability to understand the genetic basis of behaviours in natural populations.

5.2 Introduction

Parental care has been recorded in a wide range of taxa including mammals, birds, amphibians, and some invertebrate phyla including arthropods, molluscs and annelids (Smiseth et al. 2012). Parental care is frequently defined as any parental trait that increases offspring fitness and the care that parents provide varies considerably between species (Clutton-Brock et al. 1991; Smiseth et al. 2012). In many cases, parental care consists only of the deposition of nutrients, antibodies, antioxidants, and other substances into an egg (Smiseth et al. 2012). However, parents of some species provide complex care consisting of a variety of behaviours, which can include the guarding of eggs and/or offspring, the provisioning of resources to offspring both prior to and after hatching or birth, and in some cases even the bequeathal of resources to and defence of offspring after nutritional independence (Scott 1980; Lane et al. 2015). Though the diversity in parental care across species is obvious, individuals of the same species often vary substantially in the care they provide to offspring. For example, bird parents frequently differ in the rate at which they provision their young (MacColl and Hatchwell 2003a; Nakagawa et al. 2007; Dor and Lotem 2010), mammalian mothers transfer varying levels of nutrition to their offspring due to differences in the quantity and quality of milk they produce (Hinde et al. 2009), and the brood defence behaviour exhibited by parents shows considerable variation in a number of species including smallmouth bass (*Micropterus dolomieu*, Hanson et al. 2009) and Ural owls (*Strix uralensis*, Kontiainen et al. 2009).

Explaining the variation in parental care behaviour that is apparent both within and between species remains an active area of research (Smiseth et al. 2012). Much work has focused on the role of ecological conditions in generating intraspecific variation in parental care and it is now clear that parental care behaviours are influenced by various aspects of the environment, including resource availability

(Ardia et al. 2006; Low et al. 2012), predation risk (Fontaine and Martin 2006; Mutzel et al. 2013), and weather conditions (Coe et al. 2015; Wiley and Ridley 2016). Intraspecific variation in parental care may also arise due to intrinsic genetic differences between individuals (Carlier et al. 1982). An improved understanding of the extent of genetic variation in parental care is important for understanding how care evolves under natural selection, but is also fundamental to improving production and welfare traits in livestock (e.g. milk yield and composition in cows (Hill et al. 1983) and sow responses to auditory stimuli from piglets (Vangen et al. 2005)). While such traits in livestock have a long history of genetic study, it is only more recently that studies of wild populations have begun to estimate heritability for parental care traits, such as the rate at which offspring are fed in birds (e.g. Freeman-Gallant and Gothstein (1999); Dor and Lotem (2010)). However, such examples remain rare, particularly for non-avian systems.

The development of the 'animal model' has been key in furthering quantitative genetic investigations of natural populations (Wilson et al. 2010; Charmantier et al. 2014). This is because it provides a flexible analytical framework that can use complex pedigrees and incorporate environmental sources of phenotypic variation. Thus, given relatedness information among individuals and appropriate phenotypic data it is now possible to estimate genetic (and other) components of phenotypic (co) variance *in situ* from field data. Nonetheless, behavioural traits have received far less attention than morphological and life history traits to date. This is presumably because quantitative genetic approaches are data hungry and collecting high volume behavioural data is generally challenging. Parental care is no exception to this. It can be difficult to observe care directly without causing disturbance that modifies behaviour, especially if offspring are cared for in a den or nest. Even when observation is possible, it can be challenging to measure or appropriately quantify the trait(s) of interest in a large sample of individuals. For instance, behavioural studies often involve many hours of focal watches on each

individual which limits the number of individuals that can be included. Thus, despite strong interest in parent-offspring conflict and coadaptation (Kilner and Hinde 2012), and well developed theory (Hadfield 2012), empirical application of quantitative genetic methods to parental care traits in the wild has been limited.

Here, we explore an indirect approach for investigating the role of genetic differences between individuals in generating variation in parental care traits. Although it may not be feasible to measure parental care traits in enough individuals to permit powerful quantitative genetic analysis, we often have large volumes of data on offspring traits, such as growth and survival. Not only are these known to determine offspring fitness, but crucially they are often subject to parental effects, which can be defined as any influence of the parental phenotype on offspring phenotype which is independent of the genes the offspring directly inherit. Given a multi-generational pedigree, it is possible to extend the animal model framework to include parental effects on offspring phenotypes, something that is now regularly done in studies of wild vertebrates. Exploration of maternal effects is important both because they can, if present but unmodelled, cause upward bias in the narrow-sense heritability (Kruuk and Hadfield 2007), but also because they can, if genetically based, play an important role in mediating evolutionary responses to selection (Lande and Kirkpatrick 1990). Using animal models, maternal genetic effects have now been shown for juvenile growth in American red squirrels (*Tamiasciurus hudsonicus*, (McAdam et al. 2002)) and lamb birth weight in Soay sheep (*Ovis aries*, Wilson et al. 2005). Importantly for current purposes, parental genetic variation for offspring performance is expected to arise from among-parent genetic variation in parental care. Therefore, predicted maternal (or paternal) genetic merits for offspring performance generated from animal models can be used to select individuals for targeted studies of parental care behaviours. Although subsequent inferences about the genetic basis of parental care variation will necessarily be subject to more assumptions and caveats than arise from

quantitative genetic analyses of behavioural data (discussed in full later), our indirect approach is potentially applicable in situations when large sample sizes are not readily obtained for behavioural phenotypes.

In this study, we ask whether estimated maternal breeding values for lamb growth predict behavioural variation over the maternal care period in St. Kilda Soay sheep. The Soay sheep system is well suited as a test case for our indirect approach for several reasons. First, lambs vary markedly in their birth weights and early growth (Clutton-Brock et al. 2004), suggesting that there is variation in the care received. Previous work has also reported significant maternal genetic effects for these, and several additional early-life traits in this population (Wilson et al. 2005; Bérénos et al. 2014). Second, although behavioural data are not available to directly characterise variation in maternal care, data necessary to characterise offspring growth have been collected for more than 30 years. Third, relatedness information, derived from high density SNP (single nucleotide polymorphism) markers, is available for more than 8000 individuals enabling the estimation of quantitative genetic parameters using the animal model. Fourth, having predicted maternal genetic merits, it is possible to target specific individuals for behavioural observations since all individuals are marked with unique ear tags.

We first fit quantitative genetic models of lamb growth to verify the presence of maternal genetic effects. We then predict maternal breeding values (subsequently MBV) from our models and use these to select a subset of females for behavioural phenotyping (in 2014 or 2015). While care is normally viewed as parental behaviour (albeit one that is often plastically adjusted in response to offspring phenotype (Royle et al. 2014)) we observed both maternal and lamb behaviours here. This is because offspring behaviours can themselves be useful proxies of parental care. For instance, suckling behaviour is frequently used as a proxy for care provided by female mammals during lactation (Cameron 1998). We hypothesise that lambs predicted to grow more quickly as a result of maternal

(genetic) effects will be provisioned differently by their mothers. Specifically we predict that mothers with high genetic merit for lamb growth will suckle lambs more and/or reject fewer sucking attempts. We also hypothesised that any variation in suckling behaviours would influence non-sucking lamb behaviours, with lambs that sucked less and/or had their sucking attempts rejected more frequently being predicted to show increased grazing behaviour.

5.3 Methods

5.3.1 Study population

The Soay sheep on the island of Hirta in the St. Kilda archipelago have been studied since the early 1960s and the intensive study of the Village Bay population commenced in 1985. Village Bay contains ∼30% of the total island population and more than 95% of sheep in Village Bay have been marked with plastic ear tags making them individually identifiable (Clutton-Brock et al. 2004). Regular mortality checks and censuses enable the monitoring of individual survival and provide information on space use. Large amounts of phenotypic data, including those needed to calculate lamb growth, are obtained through the capture of most lambs shortly after birth and of ∼60% of all individuals each August. The capture of individuals also makes it possible to take samples for genotyping, which enables the additive relatedness matrix among individuals to be determined from high density SNP (single nucleotide polymorphism) data.

5.3.2 Animal models and selection of females for behavioural phenotyping

Using ASReml-R (Butler et al. 2007) in R version 3.1.3 (R Development Core Team 2008), we built a univariate animal model to partition the variation in lamb growth into genetic (additive and maternal) and environmental components. We

calculated lamb growth as the change in weight (in grams) between birth and August measurements divided by the number of days between these measurements to account for variation in the age at which lambs were weighed. We excluded individuals that were more than five days old when their birth weight measurement was taken to minimise the effects due to age at capture. The model contained lamb sex (two level factor), litter size (two level factor - singleton or twin), the lamb's Julian birth date (covariate) and maternal age in years (linear and quadratic terms) as fixed effects. We also included a series of random effects to partition the variance in lamb growth into a number of environmental and genetic components. As standard, we assumed all random effects were drawn from normal distributions with means of zero and variance to be estimated. We fitted additive genetic merit of the lamb to estimate the additive genetic variance V_A, and the maternal genetic merit of the mother (to estimate the maternal genetic variance V_{MG}). We also modelled a direct-maternal genetic covariance term (COV_{am}). To estimate genetic (co)variance terms we used relatedness information in the form of a SNP-derived genomic relatedness matrix (GRM - see Bérénos et al. 2014 for more details) rather than inferring the additive relatedness matrix from an explicit pedigree structure. We fitted additional random effects of birth year (V_{YoB}), and maternal permanent environment (V_{ME}). While the latter should account for non-genetic sources of variation among mothers with multiple lambs in the data set field observations also suggest that closely related females often associate spatially as adults. We therefore fitted a final random effect of maternal identity associated with a matrix containing home range overlap information for all pairs of females (see Regan et al. 2017b for details). This was to reduce the risk of common environment effects at the maternal level from biasing V_{MG}.

We initially fitted our animal model in Autumn of 2014 as described above using relatedness information available for 5805 individuals born between 1985 and 2012 and growth data for lambs born prior to 2013. We found evidence for

substantial maternal genetic effects, with the term accounting for 12% (SE=4%) of the variance in lamb growth (conditional on fixed effects). Dropping the maternal genetic effect resulted in a significantly poorer model fit ($\chi^2_{(df=1)}$=22.10, P<0.001), confirming inferences from previous analyses. MBV, interpretable as the predicted deviation of a lamb's growth from the fixed-effect mean as a result of maternal genes (over and above additive inheritance) were predicted by BLUP (Best Linear Unbiased Prediction).

Using these predictions we compiled a list of 60 females, aged between three and eight years and known to be alive in summer 2014, with the intention of selecting the upper and lower thirds of the predicted breeding value distributions for behavioural observations in the summer of 2015. In practice the eventual data structure differed somewhat from this for several reasons. First, only females surviving over winter and giving birth in the spring were available for selection. Second, because twinning rate was low (12% of litters in 2015) we decided to limit behavioural work to mother-singleton pairs only to avoid having to control for litter size effects. Third, we elected to opportunistically increase our sample size by including existing behavioural data collected in 2014 as part of another study (see Regan et al. 2017b for details). For those females observed in 2014, MBV were thus predicted after behavioural observations in the field, although we stress the genetic analysis conducted was "blind" to behavioural variation. Based on a combination of MBV and pragmatic considerations we thus selected a total of 64 females for behavioural observation (2015) and/or analysis (2014 and 2015). These were categorised as either high MBV (females with MBV >3 g.day^{-1}) or low MBV (females with MBV <-1 g.day^{-1}. See Fig. 5.1 for the distribution of MBV.

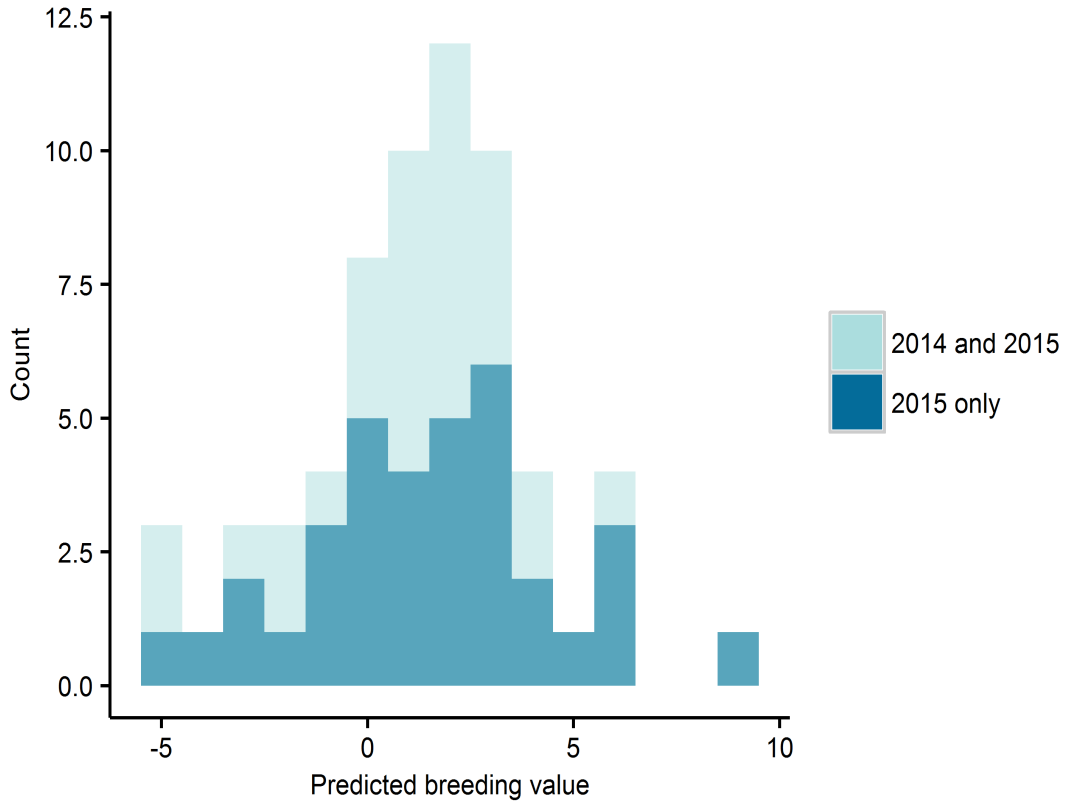

Figure 5.1: Histograms of the predicted maternal breeding values for lamb growth when considering only individuals observed in 2015 and those observed in either 2014 or 2015.

After observations had been completed we used an updated pedigree, that included individuals born between 2013 and 2016, and lamb growth data for all years preceding the year of observation (either 2014 or 2015), to get more accurate breeding value predictions. This updated pedigree included 8224 individuals (7169 maternities and 5461 paternities) and was constructed using 315 SNPs in low linkage disequilibrium (Bérénos et al. 2014). We present the results of these analyses alongside those using only data available prior to the 2015 observations. The predicted maternal breeding values from analyses conducted prior to observation are referred to as MBV_{pre} whilst those estimated using the updated pedigree and dataset are referred to as MBV_{post}.

5.3.3 Behavioural observations and trait definition

We conducted 534 focal observations, each lasting one hour, on a total of 64 females (29 in 2014, 35 in 2015) with single lambs. We restricted our study to singletons because of low twinning rates in both years (2014 - 18%, 2015 - 12%). Observations were made over three fieldwork trips per year (April-May, June-July, July-August) to monitor the behaviour of mothers and their lambs across the maternal care period. Mother-lamb pairs were observed between two and thirteen times with an average of 8.3 per pair. We used binoculars (10x42 - Vortex, USA) and spotting scopes (16-48x - Opticron, UK) to locate individuals and subsequent observations were conducted from a distance of at least ten metres to minimise disturbance. During each one hour observation we used 'Animal Behaviour Pro' (Newton-Fisher 2012) to continuously record lamb behaviour, noting whether the lamb was sucking, grazing, resting, or playing, whilst also recording whether the mother was grazing, resting, or moving at two minute intervals (see Table 5.1 for descriptions of the behaviours recorded). Observations took place between 08:00 and 19:00 and the observations of each individual were distributed across the day and between observers (two at any one time) as much as possible to prevent any bias caused by the data collection procedure. Where mothers and lambs separated during an observation, we preferentially kept the lamb in view to accurately record non-sucking behaviours. If either the mother or her lamb entered a cleit (dry-stone structures used for storage by the St. Kildans), we recorded them as 'Out of sight', as in this case we could be sure that no suckling events were missed. However, we terminated observations when both mother and lamb entered a cleit and excluded them from further analysis. There was one case in which a female (BR501) and her lamb died shortly after their second observation and we present results including these data as their inclusion did not alter any results. In addition, there was one example of a lamb sucking from both its mother and grandmother and in this case

all sucks from the grandmother were removed prior to analysis.

From each focal observation, we calculated suckling frequency (the number of suckling events), total sucking time (the time in seconds that a lamb spent sucking), mean suckle duration (total sucking time divided by the suckling frequency), suckling success [the proportion of successful suckling events (failed suckling events were classified as being shorter than five seconds following Hass (1990); Birgersson and Ekvall (1994); Tollefson et al. (2011))], and the frequency of maternally terminated suckling events (the number of suckling events that were terminated by the mother). When calculating these variables, we removed one suckling event that lasted 252 seconds as it was a clear outlier, having resulted from human disturbance. We also characterised non-suckling behaviours of both the mother and lamb. For the mother, we calculated the frequency of sampling points in which she was grazing, resting and moving (hereafter referred to as grazing frequency, resting frequency and moving frequency respectively). For the lamb, we calculated the total time that it spent grazing, playing and resting during each observation (subsequently referred to as grazing time, playing time and resting time, respectively).

Table 5.1: Descriptions of the female and lamb behaviours recorded during focal observations.

Individual	Behavior	Description
Lamb	Sucking	Recorded each time the lamb was in contact with the teat. The head is usually tilted upwards slightly and sucking is often accompanied by tail wagging and intense butting of the teat. Failed suckling events were classed as periods of suckling behaviour that lasted less than five seconds. For each suckling event, termination by either the female or lamb was noted. Female termination was characterised by the female walking off or kicking the lamb, whereas lamb termination was noted when the lamb stopped sucking of its own accord.
Lamb	Grazing	Short periods of head down movement, but where lambs were explicitly seen taking bites of grass (in the first few days of life they show interest in grass but are yet to take it into their mouth).
Lamb	Resting	When the lamb is lying down.
Lamb	Playing	Either lone play or play involving other lambs, generally characterized by short bursts of running, leaping, and head butting.
Lamb	Other	A category for all behaviours that do not fit into the other described categories. It generally consists of movement behaviour.
Lamb	Out of sight	This category was used to note periods when the lamb was not in view, whether this was because the lamb was obscured by an object, had gone out of sight during play, or had been disturbed in some way.
Female	Suckle	Noted when the female's behaviour was recorded during a suckling bout.
Female	Grazing	Head down, taking bites and short periods of head down movement between bites.
Female	Resting	Female lying down and ruminating or showing no observable activity.
Female	Moving	If the female was showing any movement not associated with grazing.
Female	Other	Periods of activity that do not fit in the other described categories. Largely made up of grooming and general alertness.
Female	Out of sight	Used to denote periods when the female was not in view.

5.3.4 Statistical analysis of behavioural traits

Behavioural data were analysed using linear and generalised linear mixed models using the packages lme4 (Bates et al. 2015) and glmmADMB (Skaug et al. 2006) in R version 3.1.3 (R Development Core Team 2008). We included individual identity and the observation date as random effects to account for the likely similarity between observations conducted on the same individual and on the same day. All

models also included lamb age (covariate), maternal age (covariate),and year (two level factor) as fixed effects. We compared six models to test whether the behaviour of a mother and/or her lamb was predicted by the mother's MBV for lamb growth. These models featured all combinations of the following fixed effects: a quadratic term for lamb age to determine whether a linear or non-linear relationship was a better fit to the data, the MBV group (high or low) that a female belonged to, and a first-order interaction between lamb age and MBV group to understand whether the association between a given behaviour and the MBV group that a female belonged to was dependent on the lamb's age. All covariates were mean centred and scaled to aid convergence. We used Akaike's Information Criterion corrected for small sample size (AICc) to compare models, with the best model taken to be that with the lowest AICc value (Burnham and Anderson 2002). AICc scores of all candidate models are presented in Tables 5.3 - 5.6.

We used linear mixed models assuming a Gaussian error distribution for resting time, grazing time, and total sucking time (with and without failed suckling events) though grazing time and sucking time were log transformed to ensure that the residual distribution was closer to normality. All other behaviours were analysed using generalised linear mixed models. Suckling frequency (with and without failed suckling events), grazing frequency, resting frequency, and moving frequency were analysed using negative binomial mixed models (in glmmADMB) because of overdispersion apparent in the residuals when errors were assumed to approximate a Poisson distribution. We assumed a binomial distribution in the case of suckling success, with the 'bobyqa' optimiser used to aid convergence. Results for playing time and the proportion of suckling events terminated by the female are not presented because severe zero-inflation resulted in poor model performance.

5.3.5 Bivariate animal models

The above approach allows us to explore the covariance between the predicted maternal breeding values and the mother/lamb behaviours. However, this will not be equal to the covariance between the true maternal breeding values for lamb growth and the true maternal breeding values for each of the behaviours. This is because breeding values are estimated with error and tend to be more correlated with an individual's phenotype than the true breeding value because an individual's predicted breeding value is determined both by it's true breeding value and environmental determinants of its phenotype (Postma 2006). As a result, any observed relationship between the predicted breeding values and behavioural traits may reflect differences between individuals in the environmental component of their phenotype, rather than purely genetic differences between them (Postma 2006; Hadfield et al. 2010).

Bivariate animal models for lamb growth and each behavioural trait make it possible to estimate parameters (e.g. the additive genetic variance) for each trait in isolation, but also provide estimates of covariance components between these traits. Explicitly estimating the maternal genetic covariance between lamb growth and each of the observed behaviours would provide the best means for understanding whether the maternal genetic effect on lamb growth was mediated by differences in maternal behaviour, but such an approach may often prove problematic. Animal models are incredibly data hungry and behavioural data, as mentioned in the introduction, are difficult and time consuming to collect. This often results in behavioural data being available for only a limited sample of animals within long-term studies, making the application of this modelling approach very difficult. Indeed, even where it is possible to use the animal model to estimate these parameters, it may be difficult to draw any substantive conclusions from the estimates given the power limitations.

We investigated the maternal genetic covariance between lamb growth and each of the behavioural traits using a series of bivariate animal models in ASReml-R. Both lamb growth and each behavioural trait were treated as a trait of the lamb and for simplicity we averaged each behavioural trait across all observations on the same individual. Furthermore, to reduce complexity and because of difficulties in assuming non-normal error distributions in ASReml we assumed Gaussian errors for all behavioural traits. To aid the convergence of models for sucking time, suckling success, and grazing time we multiplied each observation by 10. Resting time models failed to converge and therefore results of models for this trait are not presented.

The fixed and random effects for lamb growth were kept consistent with the model used to estimate the maternal breeding values prior to behavioural observation. The fixed effects were maternal age (linear and quadratic terms), lamb sex and litter size and the random effects were the additive genetic merit of the lamb, maternal genetic merit (and direct-maternal genetic covariance), maternal environment effect, birth year, and spatial overlap. To avoid complicating the model further we did not include any fixed effects for each behavioural trait, but we did incorporate additive genetic, maternal genetic and maternal environment random effects as well as terms to estimate the additive genetic covariance, maternal genetic covariance and maternal environment covariance.

Because the relatedness between the behavioural females was low (mean genomic relatedness = 0.009) it was not possible to estimate the additive genetic variance, maternal genetic variance, or maternal environment variance. Despite this, it was possible to estimate the additive genetic covariance, maternal genetic covariance, and maternal environment covariance between lamb growth and the behavioural traits. The reason that this is possible can be explained using the following example. If we consider a case where two unrelated parents are measured for one trait and their offspring are measured for a different trait, it is not possible

to estimate the additive genetic variance for the parental trait because the parents are unrelated, but it is possible to estimate the additive genetic variance for the offspring trait because the relatedness of the offspring is known. It is also possible to estimate the additive genetic covariance between the parental and offspring traits because the relatedness between parents and offspring is also known. In our case, because mothers were unrelated we needed to prevent the model from estimating the maternal variance components whilst still estimating the additive genetic covariance, maternal genetic covariance, and maternal environmental covariance between lamb growth and each behavioural trait. We did this by fixing the maternal variance components at zero whilst leaving the covariances unconstrained.

5.4 Results

5.4.1 Lamb behaviour

As expected, lamb age was an important predictor in models for all lamb behaviours, with all measures of sucking behaviour, as well as resting time, decreasing with age, whilst grazing time increased as lambs approached weaning (Table 5.2). We did find some evidence for a relationship between MBV group and lamb behaviour. This was particularly the case for suckling success, where the best fit models for this trait (using both MBV_{pre} and MBV_{post}) included MBV group (Table 5.2). In analyses using MBV_{pre} the best fit model included only a main effect of MBV group, with this term indicating that lambs born to mothers in the low MBV group had 13% fewer successful suckling bouts than those born to females in the high MBV group (Table 5.2, Fig. 5.2). Similarly, when using MBV_{post} the inclusion of the MBV group term resulted in a AICc reduction of 8.91 and also indicated that lambs born to females in the low MBV group had reduced suckling success. The inclusion of the interaction between MBV group and lamb age resulted in a further reduction of 4.05, with this term suggesting that the

reduction in suckling success with lamb age was slower for lambs born to females in the low MBV group (Table 5.2). However, this result was likely driven by reduced suckling data as lambs aged. MBV group did not feature in the best fit model for any of the other measures of lamb sucking behaviour when MBV_{pre} were used (Table 5.2); however, MBV group was included in the best fit models for suckling frequency and mean suckle duration when using MBV_{post} (Table 5.2). These models included an interaction between MBV group and lamb age, and suggested that the reduction in suckling frequency with lamb age was more pronounced for lambs born to mothers in the low MBV group (Table 5.2), whilst the reduction in mean suckle duration with lamb age was less pronounced for lambs born to mothers in the low MBV group. Nevertheless, in both cases there were simpler models that did not include MBV group and had comparable AICc values (Table 5.3 and Table 5.4) suggesting that these patterns were not particularly pronounced. It was also apparent that the variation in these behaviours between the MBV groups was driven by the differences in suckling success, with models for suckling frequency and mean suckle duration, when failed suckling events were excluded, showing there was very little difference in these behaviours between the groups (Table 5.2).

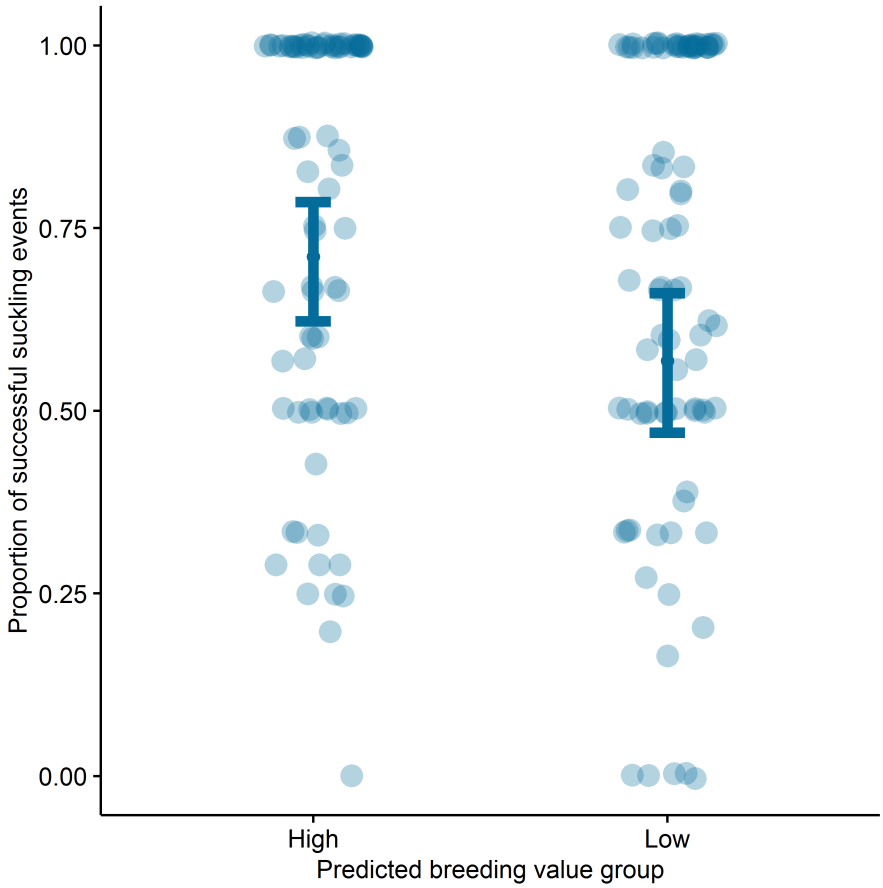

Figure 5.2: The proportion of successful suckling events was greater for lambs born to females whose predicted breeding value for lamb growth was high. Shown are point estimates and 95% confidence intervals from the best fit generalised linear mixed model using individuals observed in each of the two years and MBV_{post} breeding value predictions. To aid interpretation we plot the relationship for 2015 only.

We also found some evidence that maternal MBV predicted non-suckling lamb behaviours. Analyses of total resting time using MBV_{pre} indicated that lambs born to females in the high MBV group spent more time per hour resting. However, this model was not a markedly better fit to the data than other candidate models, given that a simpler model, lacking the MBV group term, had a comparable AICc (ΔAICc = 0.31). An association between MBV group and total resting time was more clear in analyses using MBV_{post}, with the interaction between MBV group and lamb age featuring in the best fit model (Table 5.2). This term indicated that although lambs born to females in the high MBV group spent more time resting in

the first four weeks of life, they showed a more pronounced decrease in the time they spent resting as they aged (Table 5.2, Fig. 5.3). There was some evidence that lambs born to females in the high MBV group tended to spend less time grazing, but MBV group did not feature in the best fit model for grazing time, whether MBV_{pre} or MBV_{post} were used (Table 5.2).

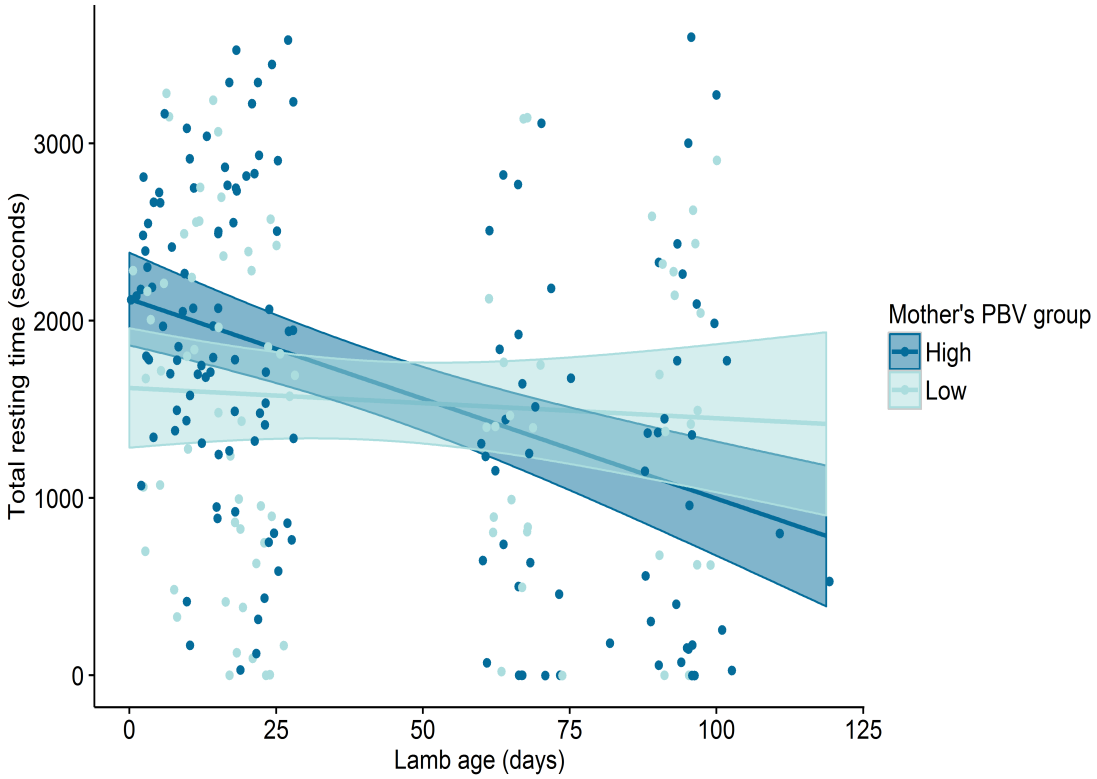

Figure 5.3: The change in lamb resting time with lamb age varied given the MBV group of their mother. Shown are the model predictions and 95% confidence intervals from the best fit model when using individuals from both years and MBV_{post}. To aid interpretation we plot the relationship for 2015 only.

Table 5.2: Parameter estimates (± standard error), AICc values, and R^2 from the best fit models for all lamb behaviours when using predicted breeding values calculated using the genomic relatedness matrix (MBV_{pre} - covering individuals born between 1985 and 2012) and the updated pedigree (MBV_{post} - covering individuals born between 1985 and 2016.

		Failed suckles included				Failed suckles excluded			
		MBV_{pre}		MBV_{post}		MBV_{pre}		MBV_{post}	
Trait	Term	Est (SE)	t/z*	Est (SE)	t/z*	Est (SE)	t/z*	Est (SE)	t/z)
Suckling frequency	Intercept	0.62 (0.25)	5.77	0.71 (0.30)	2.34	0.06 (0.27)	0.21	0.17 (0.34)	0.51
	Lamb age	−1.71 (0.32)	-5.67	-1.87 (0.30)	-6.18	-1.99 (0.31)	-6.51	-2.30 (0.29)	-7.98
	Lamb age^2	0.80 (0.34)	3.19	1.05 (0.31)	3.35	1.19 (0.33)	3.63	1.46 (0.31)	4.74
	Maternal age	0.01 (0.04)	-1.35	-0.02 (0.05)	-0.35	0.06 (0.04)	1.34	0.03 (0.05)	0.61
	Year (2015)	0.31 (0.15)	2.14	0.21 (0.17)	1.20	0.10 (0.15)	0.68	0.07 (0.19)	0.37
	MBV group (low)	-	-	0.09 (0.17)	0.54	-	-	-	-
	MBV group (low):lamb age	-	-	-0.25 (0.16)	-1.61	-	-	-	-
	AICc	880.8544	-	953.0540	-	718.7644	-	789.6522	-
Sucking time	Intercept	2.29 (0.31)	19.13	2.57 (0.36)	7.17	2.20 (0.32)	6.80	2.44 (0.36)	6.73
	Lamb age	−2.48 (0.41)	-7.50	−2.73 (0.41)	-6.68	-2.53 (0.43)	-5.91	-2.74 (0.41)	-6.70
	Lamb age^2	1.37 (0.41)	5.22	1.56 (0.41)	3.83	1.43 (0.43)	3.33	1.57 (0.41)	3.84
	Maternal age	0.10 (0.05)	0.59	0.04 (0.06)	0.79	0.09 (0.05)	1.74	0.05 (0.06)	0.95
	Year (2015)	0.22 (0.18)	1.19	0.17 (0.21)	0.81	0.25 (0.19)	1.34	0.16 (0.21)	0.76
	AICc	698.2736	-	794.9338	-	713.5273	-	801.7487	-
Mean suckle duration	Intercept	2.19 (0.22)	11.51	2.34 (0.21)	10.97	2.67 (0.18)	14.49	2.77 (0.20)	13.76
	Lamb age	−0.97 (0.26)	-3.27	-1.00 (0.27)	-3.74	-1.00 (0.17)	-5.99	-0.87 (0.17)	-5.00
	Lamb age^2	0.82 (0.28)	2.91	0.70 (0.27)	2.57	0.78 (0.18)	4.42	0.64 (0.18)	3.49
	Maternal age	0.06 (0.04)	1.81	0.05 (0.03)	1.59	0.02 (0.03)	0.61	0.01 (0.03)	0.46
	Year (2015)	0.01 (0.13)	0.06	-0.05 (0.13)	-0.37	0.12 (0.11)	1.14	0.08 (0.12)	0.69
	MBV group (low)	-	-	-0.02 (0.11)	-0.15	-	-	-	-
	MBV group (low):lamb age	-	-	0.26 (0.12)	2.21	-	-	-	-
	AICc	357.1196	-	398.3381	-	211.51	-	260.0003	-
Suckling success	Intercept	0.20 (0.37)	1.96	0.48 (0.37)	1.30	-	-	-	-
	Lamb age	−1.29 (0.53)	-3.43	−1.48 (0.54)	-2.76	-	-	-	-
	Lamb age^2	1.61 (0.61)	3.79	1.50 (0.59)	2.54	-	-	-	-

	Maternal age	0.24 (0.07)	1.61	0.14 (0.05)	2.60	-	-	-	-
	Year (2015)	−0.60 (0.23)	-2.64	−0.34 (0.23)	-1.51	-	-	-	-
	MBV group (low)	−0.62 (0.22)	-2.80	−0.15 (0.29)	-0.52	-	-	-	-
	MBV group (low):lamb age	-	-	0.79 (0.34)	2.36	-	-	-	-
	AICc	413.0004	-	422.0298	-	-	-	-	-
Resting time	Intercept	1698.84 (236.50)	7.34	1500.13 (258.16)	5.81	-	-	-	-
	Lamb age	−825.19 (332.41)	-2.72	−389.51 (80.05)	-4.87	-	-	-	-
	Lamb age^2	690.44 (333.18)	2.27	-	-	-	-	-	-
	Maternal age	21.61 (41.22)	0.64	19.75 (39.03)	0.51	-	-	-	-
	Year (2015)	−152.47 (151.65)	-1.01	50.08 (157.74)	0.32	-	-	-	-
	MBV group (low)	−223.37 (135.25)	-1.65	−111.51 (123.43)	-0.90	-	-	-	-
	MBV group (low):lamb age	-	-	330.45 (124.93)	2.65	-	-	-	-
	AICc	3477.394	-	3825.594	-	-	-	-	-
Grazing time	Intercept	5.59 (0.54)	11.26	5.56 (0.56)	9,94	-	-	-	-
	Lamb age	7.01 (0.71)	10.74	6.81 (0.63)	10.77	-	-	-	-
	Lamb age^2	−5.35 (0.72)	-8.28	−4.92 (0.63)	-7.78	-	-	-	-
	Maternal age	−0.08 (0.09)	0.16	−0.10 (0.09)	-1.10	-	-	-	-
	Year (2015)	−0.33 (0.34)	-0.95	−0.41 (0.33)	-1.23	-	-	-	-
	AICc	883.0822	-	1001.120	-	-	-	-	-

Table 5.3: AICc values for all models used in the analysis of each lamb behaviour when MBV groups were assigned using MBV_{pre}. The AICc of the best fit model in each case is shown in bold.

Model	Fixed effects	Suckling frequency	Sucking time	Mean suckle duration	Suckling success	Resting time	Grazing time
1	Lamb age+maternal age+year	884.4005	706.6290	362.9555	421.4752	3479.279	924.5436
2	Lamb age+lamb age^2+maternal age+year	**880.8544**	**698.2736**	**357.1196**	417.1164	3477.394	**883.0822**
3	Lamb age+maternal age+year+MBV group	886.5024	708.6934	364.5127	417.3880	3478.918	925.0953
4	Lamb age+lamb age^2+maternal age+year+MBV group	882.9580	700.2761	358.9977	**413.0004**	**3477.085**	883.6712
5	Lamb age+maternal age+year+MBV group+MBV group:lamb age	888.1000	710.1868	366.7163	419.1556	3478.611	927.2031
6	Lamb age+lamb age^2+maternal age+year+MBV group+MBV group:lamb age	884.5855	701.4439	361.2325	414.8227	3477.182	885.8373

Table 5.4: AICc values for all models used in the analysis of each lamb behaviour when MBV groups were assigned using MBV_{post}. The AICc of the best fit model in each case is shown in bold.

Model	Fixed effects	Suckling frequency	Sucking time	Mean suckle duration	Suckling success	Resting time	Grazing time
1	Lamb age+maternal age+year	961.7042	805.4521	402.1157	437.4242	3828.895	1046.115
2	Lamb age+lamb age^2+maternal age+year	953.1366	**794.9338**	398.9267	428.6072	3829.069	**1001.120**
3	Lamb age+maternal age+year+MBV group	962.5366	807.5141	403.7207	434.9874	3830.233	1048.013
4	Lamb age+lamb age^2+maternal age+year+MBV group	953.5185	796.8605	400.7427	426.0547	**3825.594**	1002.964
5	Lamb age+maternal age+year+MBV group+MBV group:lamb age	961.6365	809.3207	402.3034	426.0807	3830.446	1050.154
6	Lamb age+lamb age^2+maternal age+year+MBV group+MBV group:lamb age	**953.0540**	798.9033	**398.3381**	**422.0298**	3825.683	1005.121

5.4.2 Maternal behaviour

As for the lamb behaviours, lamb age was important in explaining variation in the female's behaviour, particularly in the case of grazing frequency which decreased over the maternal care period and resting frequency which decreased as lambs approached weaning (Table 5.7). We generally found little evidence that a female's MBV for lamb growth predicted her behaviour over the maternal care period. The MBV group term did not feature in the best fit models for moving frequency, grazing frequency, or resting frequency, whether we used MBV_{pre} or MBV_{post} (Table 5.7).

5.4.3 Bivariate animal models

Bivariate models for lamb growth and behavioural traits provided little evidence for significant maternal genetic or maternal environment covariances between these traits (Table 5.8). The inclusion of the covariance term failed to improve model fit in the case of sucking time ($\chi^2_{(df=1)}$=0.26, P=0.61), suckling frequency ($\chi^2_{(df=1)}$=0.08, P=0.78), mean suckle duration ($\chi^2_{(df=1)}$=3.44×e^{-6}, P=0.998), or suckling success ($\chi^2_{(df=1)}$=0.20, P=0.65). The only exception was grazing time where the inclusion of the maternal genetic covariance term marginally improved model fit ($\chi^2_{(df=1)}$=3.95, P=0.047), providing evidence for a negative maternal genetic covariance between grazing time and lamb growth. We also found little support for significant non-zero additive genetic covariances between lamb growth and any of the behavioural traits, with the incorporation of the covariance term only marginally improving model fit in the case of suckling duration ($\chi^2_{(df=1)}$=4.38, P=0.036) and suckling success ($\chi^2_{(df=1)}$=4.62, P=0.032), indicating a small positive and small negative additive genetic covariance between the traits respectively.

Table 5.5: AICc values for all models used in the analysis of each maternal behaviour when MBV groups were assigned using MBV_{pre}. The AICc of the best fit model in each case is shown in bold.

Model	Fixed effects	Grazing frequency	Moving frequency	Resting frequency
1	Lamb age+maternal age+year	**1440.300**	**554.5477**	**995.1637**
2	Lamb age+lamb age^2+maternal age+year	1442.379	556.3890	997.3110
3	Lamb age+maternal age+year+MBV group	441.917	556.1550	996.3850
4	Lamb age+lamb age^2+maternal age+year+MBV group	1444.034	558.0484	998.5164
5	Lamb age+maternal age+year+MBV group+MBV group:lamb age	1441.534	557.1884	997.5404
6	Lamb age+lamb age^2+maternal age+year+MBV group+MBV group:lamb age	1443.684	559.0182	999.5902

Table 5.6: AICc values for all models used in the analysis of each maternal behaviour when MBV groups were assigned using MBV_{post}. The AICc of the best fit model in each case is shown in bold.

Model	Fixed effects	Grazing frequency	Moving frequency	Resting frequency
1	Lamb age+maternal age+year	**1581.278**	**590.6396**	**1075.282**
2	Lamb age+lamb age^2+maternal age+year	1583.328	592.6818	1077.212
3	Lamb age+maternal age+year+MBV group	1583.276	592.6318	1076.848
4	Lamb age+lamb age^2+maternal age+year+MBV group	1585.321	594.7096	1078.721
5	Lamb age+maternal age+year+MBV group+MBV group:lamb age	1584.663	592.6676	1078.201
6	Lamb age+lamb age^2+maternal age+year+MBV group+MBV group:lamb age	1586.769	594.7693	1079.825

Table 5.7: Parameter estimates (± standard error) and AICc values from the best fit models for all female behaviours when using predicted breeding values calculated using the genomic relatedness matrix (covering individuals born between 1985 and 2012) and the updated pedigree (covering individuals born between 1985 and 2016).

		2014 and 2015 animals			
		MBV_{pre}		MBV_{post}	
Trait	Term	Est (SE)	t/z*	Est (SE)	t/z*
Grazing frequency	Intercept	3.08 (0.09)	34.11	3.10 (0.10)	32.53
	Lamb Age	−0.12 (0.02)	-4.84	−0.11 (0.02)	-4.78
	Maternal age	−0.00 (0.01)	-0.20	−0.00 (0.01)	-0.31
	Year (2015)	0.02 (0.05)	0.29	0.00 (0.06)	0.03
	MBV group (low)	-	-	-	-
	MBV group (low):lamb age	-	-	-	-
	AICc	1440.300	-	1581.278	-
Moving frequency*	Intercept	−0.98 (0.47)	-2.08	−1.27 (0.58)	-2.19
	Lamb Age	−0.01 (0.09)	-0.09	0.20 (0.09)	2.32
	Maternal age	0.08 (0.08)	1.03	0.09 (0.09)	1.05
	Year (2015)	0.55 (0.27)	2.06	0.61 (0.34)	1.79
	AICc	554.5477	-	590.6396	-
Resting frequency	Intercept	1.98 (0.49)	4.03	1.48 (0.52)	2.84
	Lamb Age	0.45 (0.14)	3.28	0.44 (0.14)	3.18
	Maternal age	−0.04 (0.08)	-0.53	0.04 (0.08)	0.44
	Year (2015)	−0.34 (0.29)	-1.16	−0.27 (0.32)	-0.82
	AICc	995.1637	-	1075.282	-

* Moving frequency models using data from both 2014 and 2015 and MBV_{post} did not include data as a random effect due to convergence problems.

Table 5.8: Estimates of additive genetic, maternal genetic, and maternal environment covariances from bivariate models of lamb growth and each behavioural trait

	Covariance term - Est (SE)		
Behavioural trait	Additive genetic	Maternal genetic	Maternal environment
Sucking time	14.87 (842.78)	185.46 (618.29)	-477.57 (754.21)
Suckling frequency	0.59 (4.98)	1.99 (3.63)	6.05 (4.03)
Mean suckle duration	39.41 (15.98)	-0.03 (16.48)	-1.28 (18.02)
Suckling success	-6.41 (2.78)	-1.32 (2.76)	-1.25 (2.96)
Grazing time	-7107.72 (3911.92)	-12362.62 (2689.30)	4789.28 (3902.01)

5.5 Discussion

Here we show that maternal predicted breeding values for lamb growth did predict variation in some behaviours associated with parental care in Soay sheep using a novel approach that combines information from the quantitative genetic animal model with targeted behavioural observations that could not logistically be conducted on the whole population. Lambs born to mothers with high predicted breeding values had a greater proportion of successful suckling events, with this tending to be most pronounced in the first weeks of life. This seemed to be associated with lambs spending more time resting per hour of observation. These results may suggest that females with higher predicted breeding values for lamb growth were able to better meet the nutritional requirements of their offspring and that, as a result, their lambs did not spend as much time closely following their mother. There was little evidence that a female's predicted breeding value predicted suckling frequency, mean suckle duration, or total sucking time, particularly once failed suckling events were excluded, suggesting that there might be variation in the amount of nutrition a lamb received per suckling event. This may be because of differences between females in the milk they produced over the maternal care period, but further work is needed to confirm whether differences in milk quality or quantity were the cause of the patterns in suckling behaviour observed here.

There has been relatively little work examining the role of genetic differences in generating variation in the parental care shown by individuals living under natural conditions, with only a small number of studies demonstrating that traits such as yolk and egg mass (Tschirren et al. 2009) and the rate at which passerine parents feed their offspring (MacColl and Hatchwell 2003a) are significantly heritable. Such studies are important for establishing the role of genetic differences between individuals in generating the parental care variation apparent in nature, thereby

advancing our understanding of how parental care responds to selection in natural systems. Suck work is important given the potential environmental dependence of heritability estimates (Weigensberg and Roff 1996; Charmantier and Garant 2005) and the need to use empirical data on parental and offspring traits to develop the quantitative genetic models that provide the theoretical basis for studying the evolution of parental care (Hadfield 2012). Though our work is unable to explicitly estimate the genetic basis of the behavioural traits observed it does provide some indirect evidence that genetic differences between female Soay sheep is associated with variation in behaviour over the maternal care period, suggesting that variation in these traits is involved in the pathway that generates maternal genetic effects on lamb growth in this population. However, our bivariate models did not suggest significant non-zero maternal genetic covariances between lamb growth and any of our behavioural traits. Although estimates of these covariances would provide the best evidence that maternal genetic effects were mediated by differences in maternal care behaviour, performing these analyses when behavioural data are limited (and/or are available on individuals with low relatedness) is unlikely to be straightforward, for example requiring assumptions to be made about some parameters (such as for the behavioural variances in our case) and limitations in terms of model complexity. This may make it difficult to draw conclusions from the derived estimates, with it being possible that the covariance estimates produced from our models reflect our relatively limited behavioural data. Indeed, it is because collecting behavioural data on the scale needed to conduct animal models is difficult that the approach put forward in this work is of interest, using estimates from the animal model to direct behavioural sampling. Although we advocate that bivariate models remain the most appropriate way to study the genetic covariances between traits, our approach may be useful as a first step in the process of studying the genetics of difficult to measure traits, such as behaviour, when there are data available to parameterise an animal model for another trait which is believed to be

associated with the trait(s) of interest. Such an approach may serve as the starting point for a more exhaustive sampling scheme if predicted breeding values were found to predict variation in the trait(s) measured in the selected subset of individuals.

The number of long-term individual-based studies of natural populations has been steadily increasing since the first studies on birds began in the 1940s, and though they are, to our knowledge, largely restricted to mammals and birds they now cover a range of species that vary substantially in the parental care provided, including passerines (Verhulst et al. 1997), seabirds (Grist et al. 2014), marsupials (Gélin et al. 2013), and primates (Alberts et al. 2003). Many of these studies are likely to have the data necessary to calculate a suitable proxy for parental care, thereby making the approach we have used in this paper tractable also in these systems. Offspring growth is likely to be one of the most important and widely available measures of offspring performance for two reasons. First, many long-term studies involve the capture of offspring shortly after birth or hatching and before weaning or fledging, thereby providing data on growth for a large number of individuals. Second, offspring growth in both birds and mammals is likely to be closely linked with the investment of parents into care given that offspring of many species are entirely reliant on the resources available from the parent(s) early in life (Clutton-Brock et al. 1991). Our approach provides a promising way to begin to study the genetic basis of parental care in the wild, but it may also prove beneficial to use the approach to direct studies when appropriate data for semi-captive populations is available. This may be particularly useful for taxa other than mammals and birds where it is very difficult to establish long-term individual based studies. In doing so, it may be possible to begin to understand the role of genetics in generating variation in a more complete range of parental care patterns.

The use of the animal model to direct field sampling on a subset of individuals could also provide a starting point for understanding how genetic differences

between individuals results in variation in traits other than those associated with parental care. In our case, we started by estimating the maternal genetic effect [a special case of indirect genetic effects (IGEs)] on lamb growth, however, it is possible that this approach could be used whenever the interest is in how the genotype of a specific individual influences the phenotype of an interacting individual by modelling different IGEs. Indeed, studies on wild populations are beginning to incorporate a wider range of indirect genetic effects into the animal model. For example, Wilson et al. (2011) modelled the indirect genetic effect on social dominance in wild red deer (*Cervus elaphus*), showing that the outcome of contests among females and young males was determined by the genes of both the focal individual and its opponent. Similarly, laying date in female common gulls (*Larus canus*) is influenced by both male and female genetics, with genes for earlier laying dates in females associated with genes for later laying dates in males (Brommer and Rattiste 2008). This work shows that, given an appropriate pedigree and a suitable proxy for the trait of interest, our approach could be used to begin to understand whether an individual's estimated genetic merit for a trait of an interacting individual predicts how it behaves towards this individual. This could include understanding how the genes carried by an individual's mate influences their reproductive investment or the ways in which individual genetics influence competitive behaviours, such as dominance or aggression, or social behaviours, such as cooperative breeding or anti-predator behaviours.

It is important to note that the breeding values we used to select individuals are only predictions (generated by BLUP) and will necessarily be associated with error and bias (Postma 2006; Hadfield et al. 2010). Statistical hypothesis testing can be massively anti-conservative when BLUP are treated as response variables and the uncertainty around them is ignored, a practice that has been shown to be problematic in both evolutionary and behavioural studies (see Hadfield et al. 2010 and Houslay and Wilson 2017). Here we advocate use of BLUP as a basis for

selecting individuals for more targeted study, and (analytically) are treating them as a predictor rather than response variables. Nonetheless, we reiterate that the relationships found are between predicted (as opposed to actual) maternal genetic merits and the observed behaviours and that the accuracy of these estimates is unknown. The accuracy of predicted breeding values is determined by the information available, for example the extent to which data are available for individuals of varying degrees of relatedness (Postma 2006). However, because observations on the focal individual and its close relatives contribute most information to the prediction of breeding values, predicted breeding values tend to be more closely correlated with the phenotypic observations than true breeding values (Postma 2006; Hadfield et al. 2010). This means that that an individual's predicted breeding value is, at least to some extent, determined by environmental effects on the individual's phenotype. Thus, although we found that predicted maternal breeding values for lamb growth predict variation in behaviour over the maternal care period our approach cannot explicitly demonstrate that the behaviours we recorded are genetically determined.

The utility of the approach we have put forward in this paper also depends on a number of additional factors. First, careful consideration must be given to the choice of proxy because the ability to draw any conclusions about the link between predicted breeding values and the trait of interest hinges upon the relationship between the proxy and that trait. For example, although offspring growth is likely to be a useful proxy when investigating the genetic basis of parental care traits, it might be optimal to use a growth measure that corresponds to the period before offspring start obtaining nutrition for themselves. Furthermore, it is important to recognise that it will likely be impossible to measure all the possible traits underlying the estimated parental genetic effect. For example, we are unable to comment on the degree to which specific maternal traits (e.g. milk quality and quantity) resulted in the behavioural patterns we observed. Second, and somewhat

related to concerns surrounding the accuracy of predicted breeding values, using the animal model to select individuals relies on the ability to parametrise an appropriate model, which itself is heavily dependent on the relatedness and phenotypic data available. Pedigrees from natural populations are often complex and incomplete and the accuracy and structure of the pedigree, as well as the availability of phenotypic data for individuals contained within the pedigree, will influence the power to estimate specific parameters and the precision of these estimates (Clément et al. 2001; Kruuk 2004; Kruuk and Hadfield 2007; Wilson et al. 2010). For example, to estimate maternal genetic effects pedigree data must span at least three generations and related individuals that have different mothers must be represented in the pedigree and phenotypic data (Kruuk and Hadfield 2007). It is possible to assess the ability to estimate specific parameters given an available pedigree and to understand the effect of missing or erroneous pedigree links using the package 'pedantics' (Morrissey and Wilson 2009). It is also important to realise that, in order to derive unbiased genetic variance component estimates, there must be sufficient data to reliably account for confounding environmental effects such as year of birth or measurement effects (Kruuk and Hadfield 2007). The animal model makes it possible to account for environmental causes of similarity between relatives, however, as with the ability to partition different genetic components of variance, the feasibility of doing so is limited by the availability of data (Kruuk and Hadfield 2007).

In summary, by using an animal model of lamb growth to select females whose genotypes were associated with differing lamb growth rates, we have been able to show that lamb behaviour differed between individuals born to females with different predicted maternal genetic merits. Further work will be needed to establish the more specific maternal traits underlying the differences in behaviour we observed here and to provide better estimates of the genetic basis of maternal care in this population. Though the approach used in this paper requires

considerable relatedness and phenotypic data, the number of long-term studies which have these data is continuing to increase. As a result, we believe that using animal model estimates to target the collection of phenotypic data from a subset of animals has the potential to advance our understanding of the role of genetics in generating trait variation in natural populations.

Chapter 6

General discussion

The aim of this thesis was to understand whether the reproduction of female Soay sheep, and in particular the parental care they provide, was influenced by their space use and their genetics. I found no association between a mother's home range quality and the behaviour of either her or her lamb during the maternal care period (Chapter 2). This might be expected to lead to females with poorer quality home ranges experiencing greater costs of reproduction because they may lack the resources necessary to offset their investment into reproduction. However, I found no evidence that home range quality influenced the survival or reproductive costs experienced by females (Chapter 3). I did find evidence that variation in space use influenced other aspects of female reproduction or the early-life traits of a female's lamb(s). Females with higher quality home ranges were more likely to bear twin litters (Chapter 3), and this result may explain the previously documented link between home range quality and female lifetime reproductive success (Regan et al. 2016). Furthermore, I found that females with more similar home ranges had lambs that were more similar in their birth dates, birth weights, and August weights (Chapter 4), suggesting that these traits were influenced by some aspect of the environment that varied across Village Bay. The quantitative genetic analyses that demonstrated a role of home range overlap in explaining the variation in these offspring traits also indicated that maternal genetic effects were an important source of variation in lamb growth (Chapter 4). By using predicted maternal breeding values from these analyses of lamb growth, I was also able to provide indirect evidence that the maternal genetic effect on lamb growth was mediated by differences in maternal care behaviour (Chapter 5). This suggests that genetic differences between females are associated with behavioural variation over the maternal care period. Together, these results indicate that differences between female Soay sheep, in terms of their genetics and space use, are associated with between-individual variation in reproduction, but that genetic differences are more strongly associated with parental care variation than differences in space use.

6.1 Incorporating movement ecology into studies of reproductive variation

Fully understanding how animal movement links environmental conditions to fitness variation will be challenging, largely because the data necessary to do so are so difficult to obtain. The excellent data available for the St. Kilda Soay sheep system made it possible for me to make a step towards bridging this gap by investigating the relationships between the space use of individual female Soay sheep and aspects of their reproduction. As mentioned previously, I found no evidence for a significant relationship between a mother's home range quality and lamb sucking behaviour, suggesting that females with access to vegetation of differing qualities do not provision their lambs differently. Although behavioural measures of mammalian maternal care may not accurately represent a mother's investment during lactation (summarised in Cameron (1998)), this result was supported by the fact that neither lamb growth between birth and weaning nor maternal body condition in August differed according to a mother's home range quality. There was no evidence that female's with home ranges of varying qualities experienced differing costs as a result of reproduction, but females with high quality home ranges were more likely to give birth to twin litters. Together, these results provide insights into the potentially complex relationships between individual space use and individual life-history traits, such as those related to reproduction.

For many reasons, I expected that a female Soay sheep's space use would be associated with her reproductive effort. First, many aspects of female reproduction are linked with body mass, including breeding probability in early-life, twinning probability, and lamb birth weight (Clutton-Brock et al. 2004). Second, Soay sheep are capital breeders, relying on stored resources to finance their reproduction (Moen et al. 2006). Because capital breeders rely on summer resources to build up

their stored fat before their next reproductive attempt, the quality of the summer range is expected to be very important (Moen et al. 2006). Third, previous research has shown that demographic traits vary across the study area, suggesting that this was likely driven by spatial variation in food quality and quantity (Coulson et al. 1999). This suggests that spatial variation in vegetation quality/quantity is likely to be associated with variation in survival and reproduction. Finally, I had previously investigated the relationship between a female's lifetime home range quality and her lifetime reproductive success, finding that females with higher quality home ranges successfully weaned more lambs over their lifetime (Regan et al. 2016). Despite having these reasons to expect a significant association between home range quality and female reproduction, I found relatively little evidence that females with home ranges of differing qualities varied in their reproduction, other than in their probability of twinning.

I argue that the most likely explanation for my results being somewhat counter-intuitive is that resources are plentiful during the summer. Crawley et al. (2004) suggests that resources in Village Bay are not limiting during the summer and individuals thus experience little resource competition. Therefore, even though Soay sheep females rely on summer resources to regain the mass lost during gestation and lactation, it is likely that all females are able to garner the resources necessary to offset their investment into reproduction. This illustrates that it will be important for future work to consider the best ways to characterise space use according to the trait being studied, such as the spatial and temporal scale used. For example, it may prove fruitful to characterise the winter space use of female Soay sheep to understand how access to resources during this period influences female reproduction. The data to do this are, however, limited due to the small number of censuses during the winter and the fact that these may not be representative of individual space use throughout the entire season given that males rut during this time. Similarly, my work illustrates the importance of

considering spatial data collection methods and the effects that these may have on the ability to accurately characterise the relationships between space use and life-history traits. In the case of the Soay sheep, it is likely that we have more spatial and life-history data for individuals residing within the grassland dominated inbye because they are found within the core study area and are thus more likely to be observed and/or captured. Similarly, we tend to conduct censuses at the same time of day and under the same weather conditions, which may result in biased estimates of individual space use. Nevertheless, the data available from the St. Kilda Soay sheep project are among the best available for answering questions about the intrinsic and extrinsic determinants of life-history variation. It is my firm belief that future work will benefit from the employment of technologies pioneered by movement ecologists, such as GPS devices, within long-term individual-based studies, as such technologies have the potential to provide us with more complete information on individual space use and can even allow us to distinguish the areas used for particular activities (Owen-Smith et al. 2010; Nams 2014). Uptake of these technologies will likely increase as data accuracy continues to improve, the size of units decreases, and there are even further reductions in their price. Here, it is important to mention that 12 GPS units were trialled on St. Kilda in 2013, and although both position and accelerometer data were of high quality, the majority of tagged sheep lost or destroyed their tags shortly after attachment (Pilkington et al. 2013). Therefore, refinement of this method would be needed before any substantial deployment of this technology could take place.

Many species exhibit home ranging behaviour, showing site fidelity and restricting their movements to specific areas over long periods (Powell and Mitchell 2012). We expect there to be a link between an individual's space use and their reproductive expenditure (for example the care they provide to offspring) because home ranges are the result of an interaction between the individual's energetic requirements and the way that resources are distributed across the landscape

(Dussault et al. 2005). Nevertheless, to my knowledge, no studies have examined relationships between home range characteristics and specific aspects of reproduction, such as parental care, in order to begin to understand the role of space use in generating fitness variation.

A number of long-term studies of free-living animal populations have been able to demonstrate substantial variation in individual fitness (Slate et al. 2000; Festa-Bianchet et al. 2000; Kjellander et al. 2004), and some have even been able to demonstrate a link between individual space use and measures of reproductive success. For example, Mcloughlin et al. (2007) showed that specific habitat types were significantly associated with female lifetime reproductive success in roe deer (*Capreolus capreolus*) at Trois-Fontaines, Champagne-Ardenne, France. Similarly, research has shown associations between the selection/use of particular plant communities and the lifetime reproductive success of red deer on the isle of Rum (McLoughlin et al. 2006) and St. Kilda Soay sheep (Regan et al. 2016). At the same time, movement ecology has made substantial progress in understanding the sources of between-individual differences in movement. For instance, studies have demonstrated that home range size is explained by a variety of factors, including extrinsic factors such as spatiotemporal variation in the quantity and quality of food resources (Saïd et al. 2009; van Beest et al. 2011b; Morellet et al. 2013), climate (Morellet et al. 2013), weather (van Beest et al. 2011b; Morellet et al. 2013), as well as intrinsic factors such as an individual's age (Saïd et al. 2009), and reproductive status (van Beest et al. 2011b). Although movement ecology and evolutionary ecology have made big steps forward within their own specific areas, little work has explored the expected link between animal movement and reproductive variation, for example by characterising the associations between the space use of free-living individuals and specific components of their reproductive success, such as their investment into parental care. Establishing the exact mechanisms by which environmental variation generates life-history variation will

be necessary for explicitly understanding the consequences of environmental variation on population and evolutionary dynamics.

6.2 Understanding the genetics of parental care

Whilst working to understand how individual space use influenced maternal care, I became interested in the ways that space use patterns could influence the ability to study other sources of variation in parental care, particularly in cases where relatives share space due to natal philopatry, as in female Soay sheep. Having methods to account for the space sharing of relatives is likely to be particularly important when studying the genetic components of variation in parental care. This is because of the potential bias induced in quantitative genetic estimates when phenotypic similarity between relatives is assumed to be caused by shared genes alone when relatives also share environments (Kruuk and Hadfield 2007). Within quantitative genetics, it is routine to account for some sources of shared environment effects, such as being born in the same year (for example in Garant et al. (2005); Teplitsky et al. (2008)), or sharing the same mother (for example McAdam et al. (2002); Wilson et al. (2005)). Nonetheless, it is rare for studies to account for common environment effects arising due to relatives using space similarly.

I accounted for the space sharing by related female Soay sheep within the quantitative animal model by incorporating a matrix of pairwise home range overlap estimates and by modelling spatial autocorrelation directly. I built on previous work by studying a greater range of traits and by putting more stringent restrictions on the spatial data necessary for an individual to be included in these analyses. This was important to prevent bias being introduced by individual space use being poorly estimated and to ensure that my conclusions were not influenced by the use of traits, such as home range size, whose heritability estimates are very

likely to be biased when space sharing is not accounted for because they are spatial metrics. My results showed that in the Soay sheep, accounting for the space sharing of female relatives had little effect on the estimates of additive genetic and maternal genetic effects, and therefore heritability estimates were largely unchanged. This was not what I expected, and was in contrast to previous studies that had investigated the role of space sharing in generating phenotypic similarity (Van Der Jeugd and McCleery 2002; Stopher et al. 2012) . My results suggest that philopatry is not necessarily a source of substantial bias in quantitative genetic estimates. This has implications for research on both the Soay sheep system and other wild systems. First, the fact that studies are providing contradictory results (Van Der Jeugd and McCleery 2002; Stopher et al. 2012; Germain et al. 2016; Regan et al. 2017a) suggests that further studies will be required to delineate any clear patterns. Such trends may only become clear when studies are conducted on a greater variety of traits within a greater range of species that exhibit a broader range of dispersal patterns. Furthermore, expectations regarding the degree of bias are likely to be affected by the spatial distribution of resources, because this will dictate the extent to which individuals that share space will experience similar environments. Second, my work raises questions about the strength and patterns of philopatry in the Soay sheep system, and more widely draws attention to the intricacies of selecting appropriate methods for characterising space sharing patterns generated by processes such as natal philopatry. I think it is unlikely that my results were caused by philopatry being substantially weaker than previously documented in the Soay sheep population (Coltman et al. 2003), but it is possible that the methods currently available to characterise space sharing are not the most suitable for this system. For example, due to analytical limitations I was only able to use 100% kernel home range estimates when constructing home range overlap matrices. Outer isopleths, containing areas used less frequently, are expected to give poorer home range estimates (Seaman et al. 1999) and therefore use of the

100% isopleth may have resulted in individuals having overlap estimates that do not reflect their true spatial overlap. I would have liked to delve further into the potential causes for the results in Chapter 4, but it is clear that there is a need for continued development and trials of tools for characterising aspects of animal movement, particularly for use within other fields, such as quantitative genetics.

In Chapter 5, I used the quantitative genetic models described above to investigate the genetic determinants of parental care variation. Explicitly studying the genetics of parental care behaviour in the wild is often exceptionally difficult because time and funding constraints prevent the collection of data on large numbers of individuals. Understanding the genetics of parental care has wide-ranging implications, from furthering our understanding of the evolution of parental care, to facilitating advances in the breeding of livestock where parental care traits are of particular interest, for example milk yield and egg size. Some studies have provided heritability estimates for specific aspects of parental care measured in wild individuals. For example, a small number of studies have shown heritable variation in nesting behaviour (McGaugh et al. 2010), maternal yolk hormone transfer (Tschirren et al. 2009), and the provisioning behaviour of avian parents (Freeman-Gallant and Gothstein 1999; MacColl and Hatchwell 2003b). However, quantitative genetic studies of parental care traits in the wild remain relatively few and far between. I have shown that it may be possible to begin to understand the importance of genetic differences between individuals in generating variation in parental care, by using data that are often available within long-term studies of natural populations. In fact, the approach used in Chapter 5 has the potential to be used to understand the genetic determinants of a variety of traits that are difficult to study in the wild. This approach can be used when there is a suitable pedigree and an appropriate proxy for the trait of interest to enable the prediction of individual breeding values prior to targeted behavioural observations or other sampling. This approach does have its limitations. Perhaps the most

pronounced is that the maternal breeding values used in the analysis are predictions, and are thereby associated with error. As a result, this approach will never be able to conclusively demonstrate a genetic basis to the trait being studied. Nevertheless, given that quantitative genetic studies of parental traits themselves are currently impractical in many systems, this approach will hopefully serve as a useful starting point for more in depth studies of the genetics of traits, including parental care behaviours, in natural populations.

6.3 Where should future work go?

This thesis demonstrates the important role that long-term individual-based studies of wild populations will play in shedding light on the causes of variation in aspects of individual life-history. In particular, I have shown that the phenotype, pedigree, and space use data commonly collected as part of studies such as the St. Kilda Soay sheep project will prove invaluable for studying the effects of individual genetics and space use in generating between-individual variation in reproductive expenditure. However, an interdisciplinary approach will soon be required to provide further insights into the relationships between individual differences arising due to variation in genetics and space use, life-history variation, and population and evolutionary dynamics.

For example, I believe that tighter links between movement ecology and evolutionary ecology will be necessary to advance our understanding of the ways in which animal movement links environmental variation to individual life-histories. The possible scope of future studies will be improved by the uptake of both tracking technologies and remote sensing within the long-term studies that already provide invaluable phenotypic and life-history data. Currently, economic constraints prevent the use of tracking technology across a large number of individuals, but it may be possible to gain substantial insights by testing specific

hypotheses through small deployments. There is also a great need to remember that space use itself is dynamic, and thus that the relationship between space use and reproduction is not unidirectional. For example, some research has already shown that mammalian mothers adjust their space use in response to their reproductive status (Tufto et al. 1996; Saïd et al. 2005; Grignolio et al. 2007). Nevertheless, little is known about the relationship between an individual's reproductive success and its subsequent movement. Such understanding will not be possible without a combination of detailed movement and life-history data.

Interdisciplinary research will also be necessary to yield insights into the role of intrinsic differences between individuals, for example due to genetics, in generating parental care variation. Although long-term studies already collect data on some aspects of parental care, such as clutch size, egg mass, and offspring birth weight, the data collection within these studies tends to focus on specific subsets of predominantly morphological traits. This means we tend to lack the data necessary to understand how factors, such as genetics, contribute to the variation in specific parental care traits. By using different data collection methodologies, for example focal observations, to study specific subsets of animals within long-term studies, it will be possible to use the invaluable data already collected in these studies to ask a greater variety of questions.

It will be interesting to see how long-term studies, that have contributed so much to our understanding of life-history variation, will embrace future developments to ensure that the wealth of data collected can be applied to answer new and exciting research questions.

References

Akesson M, Bensch S, Hasselquist D, Tarka M, Hansson B. 2008. Estimating heritabilities and genetic correlations: comparing the 'animal model' with parent-offspring regression using data from a natural population. PLoS One. 3:1–10.

Alberti M. 2015. Eco-evolutionary dynamics in an urbanizing planet. Trends Ecol Evol. 30:114–126.

Alberts SC, Watts HE, Altmann J. 2003. Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. Anim Behav. 65:821–840.

Albon SD, Clutton-Brock TH, Guinness FE. 1987. Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. J Anim Ecol. 56:69.

Albon SD, Irvine RJ, Halvorsen O, Langvatn R, Loe LE, Ropstad E, Veiberg V, van der Wal R, Bjørkvoll EM, Duff EI, Hansen BB, Lee AM, Tveraa T, Stien A. 2017. Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. Glob Chang Biol. 23:1374–1389.

Allan E, Crawley MJ. 2011. Contrasting effects of insect and molluscan herbivores on plant diversity in a long-term field experiment. Ecol Lett. 14:1246–1253.

Alonso JC, Magaña M, Palacín C, Martín CA. 2010. Correlates of male mating success in great bustard leks: the effects of age, weight, and display effort. Behav Ecol Sociobiol. 64:1589–1600.

Andersen R, Gaillard JM, Linnell JDC, Duncan P. 2000. Factors affecting maternal care in an income breeder, the European roe deer. J Anim Ecol. 69:672–682.

Andrews CP, Kruuk LEB, Smiseth PT. 2016. Evolution of elaborate parental care: phenotypic and genetic correlations between parent and offspring traits. Behav Ecol.

Arcese P, Smith JNM, Smitht JNM. 1988. Effects of population density and supplemental food on reproduction in song sparrows. J Anim Ecol. 57:119–136.

Ardia DR. 2005. Tree swallows trade off immune function and reproductive effort differently across their range. Ecology. 86:2040–2046.

Ardia DR, Wasson MF, Winkler DW. 2006. Individual quality and food availability determine yolk and egg mass and egg composition in tree swallows *Tachycineta bicolor*. J Avian Biol. 37:252–259.

Bales K, French JA, Dietz JM. 2002. Explaining variation in maternal care in a cooperatively breeding mammal. Anim Behav. 63:453–461.

Banerjee S, Finley AO, Waldmann P, Ericsson T. 2010. Hierarchical Spatial Process Models for Multiple Traits in Large Genetic Trials. J Am Stat Assoc. 105:506–521.

Barbraud C, Weimerskirch H. 2005. Environmental conditions and breeding experience affect costs of reproduction in blue petrels. Ecology. 86:682–692.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw. 67:1–48.

Beamonte-Barrientos R, Velando A, Drummond H, Torres R. 2010. Senescence of maternal effects: aging influences egg quality and rearing capacities of a long-lived bird. Am Nat. 175:469–80.

Beckerman A, Benton TG, Ranta E, Kaitala V, Lundberg P. 2002. Population dynamic consequences of delayed life-history effects. Trends Ecol Evol. 17:263–269.

Bell G. 1980. The costs of reproduction and their consequences. Am Nat. 116:45–76.

Benton TG, Plaistow SJ, Coulson TN. 2006. Complex population dynamics and complex causation: devils, details and demography. Proceedings Biol Sci. 273:1173–81.

Beraldi D, McRae AF, Gratten J, Slate J, Visscher PM, Pemberton JM. 2007. Mapping quantitative trait loci underlying fitness-related traits in a free-living sheep population. Evolution. 61:1403–16.

Bérénos C, Ellis PA, Pilkington JG, Pemberton JM. 2014. Estimating quantitative genetic parameters in wild populations: A comparison of pedigree and genomic approaches. Mol Ecol. 23:3434–3451.

Bhattacharyya A. 1943. On a measure of divergence between two statistical populations defined by their probability distributions. Bull Calcutte Math Soc. 35:99–109.

Bielby J, Mace GM, Bininda-Emonds ORP, Cardillo M, Gittleman JL, Jones KE, Orme CDL, Purvis A. 2007. The fast-slow continuum in mammalian life history: an empirical reevaluation. Am Nat. 169:748–57.

Birgersson B, Ekvall K. 1994. Suckling time and fawn growth in fallow deer (*Dama dama*). J Zool. 232:641–650.

Birgersson B, Ekvall K. 1997. Early growth in male and female fallow deer fawns. Behav Ecol. 8:493–499.

Biro PA, Stamps JA. 2008. Are animal personality traits linked to life-history productivity? Trends Ecol Evol. 23:361–368.

Bize P, Devevey G, Monaghan P, Doligez B, Christe P. 2008. Fecundity and survival in relation to resistance to oxidative stress in a free-living bird. Ecology. 89:2584–2593.

Bjørnstad ON, Hansen TF. 1994. Individual variation and population dynamics. Oikos. 69:167–171.

Blank JL, Nolan V. 1983. Offspring sex ratio in red-winged blackbirds is dependent on maternal age. Proc Natl Acad Sci. 80:6141–6145.

Blundell GM, Maier JAK, Debevec EM. 2001. Linear home ranges: Effects of smoothing, sample size, and autocorrelation on kernel estimates. Ecol Monogr. 71:469–489.

Bonnet X, Lourdais O, Shine R, Naulleau G. 2002. Reproduction in a typical capital breeder: costs, currencies, and complications in the aspic viper. Ecology. 83:2124–2135.

Boutin S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Can J Zool. 68:203–220.

Bouwhuis S, Charmantier A, Verhulst S, Sheldon BC. 2010. Individual variation in rates of senescence: natal origin effects and disposable soma in a wild bird population. J Anim Ecol. 79:1251–1261.

Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol Rev. 80:205–225.

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA. 2002. Evaluating resource selection functions. Ecol Model. 157:281–300.

Brommer JE, Rattiste K. 2008. 'Hidden' reproductive conflict between mates in a wild bird population. Evolution. 62:2326–2333.

Brouwer L, van de Pol M, Cockburn A. 2014. The role of social environment on parental care: offspring benefit more from the presence of female than male helpers. J Anim Ecol. 83:491–503.

Burnham KP, Anderson DR. 2002. Information and likelihood theory: a basis for model selection. In: Burnham K, Anderson D, editors, Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. New York: Springer-Verlag New York. p. 49–97.

Burt WH. 1943. Territoriality and home range concepts as applied to mammals. J Mammal. 24:346–352.

Butler DG, Cullis BR, Gilmour AR, Gogel BJ. 2007. Analysis of Mixed Models for S Language Environments: ASReml-R Reference Manual, Release 2. Queensland Department of Primary Industries and Fisheries, Brisbane, Australia.

Byholm P, Rousi H, Sole I. 2011. Parental care in nesting hawks: breeding experience and food availability influence the outcome. Behav Ecol. 22:609–615.

Cagnacci F, Boitani L, Powell RA, Boyce MS. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philos Trans R Soc Lond B Biol Sci. 365:2157–62.

Calenge C. 2006. The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. Ecol Model. 197:516–519.

Cameron E. 1998. Is suckling behaviour a useful predictor of milk intake? A review. Anim Behav. 56:521–532.

Campbell MT, Slade NA. 1995. The effect of maternal mass on litter size and offspring survival in the hispid cotton rat (*Sigmodon hispidus*). Can J Zool. 73:133–140.

Campbell RN. 1974. St Kilda and its sheep. London: Athlone Press. p. 8–35.

Carlier M, Roubertoux P, Cohen-Salmon C. 1982. Differences in patterns of pup care in *Mus musculus domesticus* Comparisons between eleven inbred strains.

Catchpole EA, Fan Y, Morgan BJT, Clutton-Brock TH, Coulson T. 2004. Sexual Dimorphism, Survival and Dispersal in Red Deer. J Agric Biol Environ Stat. 9:1–26.

Catchpole EA, Morgan BJT, Coulson TN, Freeman SN, Albon SD. 2000. Factors influencing Soay sheep survival. Appl Stat-J Roy St C. 49:453–472.

Cauchard L, Boogert NJ, Lefebvre L, Dubois F, Doligez B. 2013. Problem-solving performance is correlated with reproductive success in a wild bird population. Anim Behav. 85:19–26.

Chapman BB, Brönmark C, Nilsson JÅ, Hansson LA. 2011. The ecology and evolution of partial migration. Oikos. 120:1764–1775.

Charmantier A, Buoro M, Gimenez O, Weimerskirch H. 2011. Heritability of short-scale natal dispersal in a large-scale foraging bird, the wandering albatross. J Evol Biol. 24:1487–1496.

Charmantier A, Garant D. 2005. Environmental quality and evolutionary potential: lessons from wild populations. Proc R Soc London B Biol Sci. 272:14151425.

Charmantier A, Garant D, Kruuk LE, editors. 2014. Quantitative genetics in the wild. Oxford, United Kingdom: Oxford University Press.

Charmantier A, Perrins C, McCleery RH, Sheldon BC. 2006. Quantitative genetics of age at reproduction in wild swans: support for antagonistic pleiotropy models of senescence. Proc Natl Acad Sci U S A. 103:6587–92.

Christians JK. 2002. Avian egg size: variation within species and inflexibility within individuals. Biol Rev Camb Philos Soc. 77:1–26.

Cichoń M, Olejniczak P, Gustafsson L. 2008. The effect of body condition on the cost of reproduction in female Collared Flycatchers *Ficedula albicollis*. Ibis. 140:128–130.

Clément V, Bibé B, Verrier E, Elsen JM, E M, Bouix J, Hanocq E. 2001. Simulation analysis to test the influence of model adequacy and data structure on the estimation of genetic parameters for traits with direct and maternal effects. Genet Sel Evol. 33:369–395.

Cliff A, Ord J. 1981. Spatial processes: models and applications. Pion, London.

Clutton-Brock TH, Albon SD. 1983. Climatic variation and body weight of red deer. J Wildl Manage. 47:1197–1201.

Clutton-Brock TH, Albon SD, Guinness FE. 1989. Fitness costs of gestation and lactation in wild mammals. Nature. 337:260–262.

Clutton-Brock TH, Pemberton JM, Coulson T, Stevenson IR, Maccoll ADC. 2004. Individuals and populations. In: Clutton-Brock TH, Pemberton JM, editors, Soay sheep: dynamics and selection in an island population. Cambridge, United Kingdom: Cambridge University Press. p. 1–13.

Clutton-Brock TH, Price OF, Albon SD, Jewell PA. 1991. Persistent instability and population regulation in Soay sheep. J Anim Ecol. 60:593–608.

Clutton-Brock TH, Price OF, Albon SD, Jewell PA. 1992. Early devlopment and population fluctuations in Soay sheep. J Anim Ecol. 61:381–396.

Clutton-Brock TH, Stevenson IR, Marrow P, MacColl AD, Houston AI, McNamara JM. 1996. Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. J Anim Ecol. 65:675.

Coe BH, Beck ML, Chin SY, Jachowski CMB, Hopkins WA. 2015. Local variation in weather conditions influences incubation behavior and temperature in a passerine bird. J Avian Biol. 46:385–394.

Cole EF, Morand-Ferron J, Hinks AE, Quinn JL. 2012. Cognitive ability influences reproductive life history variation in the wild. Curr Biol. 22:1808–1812.

Coltman DW, Pilkington JG, Pemberton JM. 2003. Fine-scale genetic structure in a free-living ungulate population. Mol Ecol. 12:733–742.

Côté SD, Festa-Bianchet M. 2001a. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia. 127:230–238.

Côté SD, Festa-Bianchet M. 2001b. Offspring sex ratio in relation to maternal age and social rank in mountain goats (*Oreamnos americanus*). Behav Ecol Sociobiol. 49:260–265.

Coulson T, Albon S, Pilkington J, Clutton-Brock T. 1999. Small-scale spatial dynamics in a fluctuating ungulate population. J Anim Ecol. 68:658–671.

Coulson T, Catchpole EA, Albon SD, Morgan BJ, Pemberton JM, Clutton-Brock TH, Crawley MJ, Grenfell BT. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science. 292:1528–1531.

Crawley MJ, Albon SD, Bazely DR, Milner JM, Pilkington JG, Tuke AL. 2004. Vegetation and sheep population dynamics. In: Clutton-Brock TH, Pemberton JM, editors, Soay sheep: dynamics and selection in an island population. Cambridge, United Kingdom: Cambridge University Press. p. 89–111.

Creighton JC, Heflin ND, Belk MC. 2009. Cost of reproduction, resource quality, and terminal investment in a burying beetle. Am Nat. 174:673–84.

Cullis BR, Gleeson AC. 1989. Efficiency of neighbour analysis for replicated variety trials in Australia. J Agric Sci. 113:233–239.

Cullis BR, Gleeson AC. 1991. Spatial analysis of field experiments-an extension to two dimensions. Biometrics. 47:1449–1460.

Daunt F, Monaghan P, Wanless S, Harris MP, Griffiths R. 2001. Sons and daughters: age-specific differences in parental rearing capacities. Funct Ecol. 15:211–216.

Debeffe L, Poissant J, McLoughlin PD. 2017. Individual quality and age but not environmental or social conditions modulate costs of reproduction in a capital breeder. Ecol Evol:5580–5591.

Delia JRJ, Ramírez-Bautista A, Summers K. 2013. Parents adjust care in response to weather conditions and egg dehydration in a Neotropical glassfrog. Behav Ecol Sociobiol. 67:557–569.

Descamps S, Boutin S, McAdam AG, Berteaux D, Gaillard JM. 2009a. Survival costs of reproduction vary with age in North American red squirrels. Proc R Soc London B Biol Sci. 276:1129–1135.

Descamps S, Gilchrist HG, Bêty J, Buttler EI, Forbes MR. 2009b. Costs of reproduction in a long-lived bird: large clutch size is associated with low survival in the presence of a highly virulent disease. Biol Lett. 5:278–281.

Dixon A, Ross D, O'Malley SLC, Burke T. 1994. Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. Nature. 371:698–700.

Doligez B, Gustafsson L, Pärt T. 2009. 'Heritability' of dispersal propensity in a patchy population. Proc R Soc Lond B Biol Sci. 276:2829–2836.

Dor R, Lotem A. 2010. Parental effort and response to nestling begging in the house sparrow: repeatability, heritability and parent-offspring co-evolution. J Evol Biol. 23:1605–1612.

Duquette L, Millar J. 1995. The Effect of Supplemental Food on Life-History Traits and Demography of a Tropical Mouse *Peromyscus mexicanus*. J Anim Ecol. 64:348.

Dussault C, Courtois R, Ouellet JP, Girard I. 2005. Space use of moose in relation to food availability. Can J Zool. 83:1431–1437.

Dutkowski GW, Costa e Silva J, Gilmour AR, Wellendorf H, Aguiar A. 2006. Spatial analysis enhances modelling of a wide variety of traits in forest genetic trials. Can J For Res. 36:1851–1870.

Dutkowski GW, Silva JCe, Gilmour AR, Lopez GA. 2002. Spatial analysis methods for forest genetic trials. Can J For Res. 32:2201–2214.

Eccard JA, Ylönen H. 2001. Initiation of breeding after winter in bank voles: effects of food and population density. Can J Zool. 79:1743–1753.

Eide N, Jepsen J, Prestrud P. 2004. Spatial organization of reproductive Arctic foxes *Alopex lagopus*: responses to changes in spatial and temporal availability of prey. J Anim Ecol. 73:1056–1068.

Ericsson G, Wallin K, Ball JP, Broberg M. 2001. Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. Ecology. 82:1613–1620.

Falconer D, Mackay TF. 1996. Introduction to quantitative genetics. 4th Edition. Prentice Hall, London.

Fay R, Barbraud C, Delord K, Weimerskirch H. 2016. Variation in the age of first reproduction: different strategies or individual quality? Ecology. 97:1842–1851.

Festa-Bianchet M, Gaillard JM, Jorgenson JT. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. Am Nat. 152:367–79.

Festa-Bianchet M, Jorgenson JT. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. Behav Ecol. 9:144–150.

Festa-Bianchet M, Jorgenson JT, Reale D. 2000. Early development, adult mass, and reproductive success in Bighorn sheep. Behav Ecol. 11:633–639.

Fieberg J, Kochanny C. 2005. Quantifying home-range overlap: the importance of the utilization distribution. J Wildl Manage. 69:1346–1359.

Fontaine JJ, Martin TE. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. Ecol Lett. 9:428–434.

Forchhammer MC, Clutton-Brock TH, Lindström J, Albon SD. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. J Anim Ecol. 70:721–729.

Freeman-Gallant CG, Gothstein MD. 1999. Apparent heritability of parental care in savannah sparrows. Auk. 116:1132–1136.

Gaillard JM, Boutin JM, Delorme D, Van G, Duncan LP, Lebreton JD. 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. Oecologia1. 112:502–513.

Gaillard JM, Festa-Bianchet M, Delorme D, Jorgenson J. 2000. Body mass and individual fitness in female ungulates: bigger is not always better. Proc R Soc B. 267:471–477.

Gaillard JM, Festa-Bianchet M, Yoccoz NG. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends Ecol Evol. 13:58–63.

Gaillard JM, Hebblewhite M, Loison A, Fuller M, Powell R, Basille M, Van Moorter B. 2010. Habitatperformance relationships: finding the right metric at a given spatial scale. Philos Trans R Soc London B Biol Sci. 365.

Gaillard JM, Yoccoz NG. 2003. Temporal variation in survival of mammals: a case of environmental canalization? Ecology. 84:3294–3306.

Garant D, Kruuk LE, Wilkin TA, McCleery RH, Sheldon BC. 2005. Evolution driven by differential dispersal within a wild bird population. Nature. 433:60–65.

Garnier A, Gaillard JM, Gauthier D, Besnard A. 2016. What shapes fitness costs of reproduction in long-lived iteroparous species? A case study on the Alpine ibex. Ecology. 97:205–214.

Gélin U, Wilson ME, Coulson GM, Festa-Bianchet M. 2013. Offspring sex, current and previous reproduction affect feeding behaviour in wild eastern grey kangaroos. Anim Behav. 86:885–891.

Germain RR, Wolak ME, Arcese P, Losdat S, Reid JM. 2016. Direct and indirect genetic and fine-scale location effects on breeding date in song sparrows. J Anim Ecol. 85:1613–1624.

Ghalambor CK, Peluc SI, Martin TE. 2013. Plasticity of parental care under the risk of predation: how much should parents reduce care? Biol Lett. 9.

Gilmour AR, Gogel B, Cullis BR, Thompson R. 2009. Asreml User Guide Release 3.0.

González-Solís J, Becker PH, Jover L, Ruiz X. 2004. Individual changes underlie age-specific pattern of laying date and egg-size in female common terns (*Sterna hirundo*). J Ornithol. 145:129–136.

Green AJ. 2001. Mass/length residuals: measures of body condition or generators of spurious results? Ecology. 82:1473–1483.

Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim Behav. 28:1140–1162.

Grignolio S, Rossi I, Bertolotto E, Bassano B, Apollonio M. 2007. Influence of the kid on space use and habitat selection of female alpine ibex. J Wildl Manage. 71:713–719.

Grist H, Daunt F, Wanless S, Nelson EJ, Harris MP, Newell M, Burthe S, Reid JM. 2014. Site fidelity and individual variation in winter location in partially migratory European shags. PLoS One. 9:e98562.

Gwynne D, Milner C, Hormung M. 1974. The vegetation and soils of Hirta. In: Jewell PA, Milner C, Boyd JM, editors, Island survivors: the ecology of the Soay sheep of St Kilda. London: Athlone Press. p. 36–87.

Hadfield JD. 2012. The quantitative genetic theory of parental effects. In: Royle N, Smiseth PT, Kölliker M, editors, The Evolution of Parental Care. Oxford, United Kingdom: Oxford University Press. p. 267–280.

Hadfield JD, Burgess MD, Lord A, Phillimore AB, Clegg SM, Owens IPF. 2006. Direct versus indirect sexual selection: genetic basis of colour, size and recruitment in a wild bird. Proc R Soc Lond B Biol Sci. 273:1347–53.

Hadfield JD, Wilson AJ, Garant D, Sheldon BC, Kruuk LEB. 2010. The Misuse of BLUP in Ecology and Evolution. Am Nat. 175:116–125.

Hadley GL, Rotella JJ, Garrott RA, Nichols JD. ???? J Anim Ecol.

Hamel S, Côté SD, Festa-Bianchet M. 2010a. Maternal characteristics and environment affect the costs of reproduction in female mountain goats. Ecology. 91:2034–2043.

Hamel S, Côté SD, Gaillard JM, Festa-Bianchet M. 2009. Individual variation in reproductive costs of reproduction: high-quality females always do better. J Anim Ecol. 78:143–151.

Hamel S, Gaillard JM, Yoccoz NG, Loison A, Bonenfant C, Descamps S. 2010b. Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. Ecol Lett. 13:915–935.

Hanson KC, O'Connor CM, Van Der Kraak G, Cooke SJ. 2009. Paternal aggression towards a brood predator during parental care in wild smallmouth bass is not correlated with circulating testosterone and cortisol concentrations. Horm Behav. 55:495–499.

Hansson B, Bensch S, Hasselquist D. 2003. Heritability of dispersal in the great reed warbler. Ecol Lett. 6:290–294.

Hare JF, Murie JO. 1992. Manipulation of litter size reveals no cost of reproduction in Columbian ground squirrels. J Mammal. 73:449–454.

Harrison F, Barta Z, Cuthill I, Székely T. 2009. How is sexual conflict over parental care resolved? A meta-analysis. J Evol Biol. 22:1800–1812.

Hass CC. 1990. Alternative maternal-care patterns in two herds of bighorn sheep. J Mammal. 71:24–35.

Hasselquist D, Kempenaers B. 2002. Parental care and adaptive brood sex ratio manipulation in birds. Philos Trans R Soc B Biol Sci. 357:363–372.

Hatchwell B, Komdeur J. 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. Anim Behav. 59:1079–1086.

Hayward AD, Moorad J, Regan CE, Berenos C, Pilkington JG, Pemberton JM, Nussey DH. 2015. Asynchrony of senescence among phenotypic traits in a wild mammal population. Exp Gerontol. 71:56–68.

Haywood S. 2008. Role of extrinsic factors in the control of clutch-size in the Blue Tit *Parus caeruleus*. Ibis. 135:79–84.

Haywood S, Perrins CM. 1992. Is clutch size in birds affected by environmental conditions during growth? Source Proc Biol Sci. 249:195–197.

Hebblewhite M, Haydon DT. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Philos Trans R Soc Lond B Biol Sci. 365:2303–12.

Heckerman D, Gurdasani D, Kadie C, Pomilla C, Carstensen T, Martin H, Ekoru K, Nsubuga RN, Ssenyomo G, Kamali A, Kaleebu P, Widmer C, Sandhu MS. 2016. Linear mixed model for heritability estimation that explicitly addresses environmental variation. Proc Natl Acad Sci. 113:7377–7382.

Hegner RE, Wingfield JC. 1987. Effects of brood-size manipulations on parental investment, breeding success, and reproductive endocrinology of house sparrows. Auk. 104:470–480.

Helfer V, Broquet T, Fumagalli L. 2012. Sex-specific estimates of dispersal show female philopatry and male dispersal in a promiscuous amphibian, the alpine salamander (*Salamandra atra*). Mol Ecol. 21:4706–4720.

Hewison A, Gaillard JM. 1999. Successful sons or advantaged daughters? The Trivers-Willard model and sex-biased maternal investment in ungulates. Trends Ecol Evol. 14:229–234.

Hewison AJM, Gaillard JM. 2001. Phenotypic quality and senescence affect different components of reproductive output in roe deer. J Anim Ecol. 70:600–608.

Hill WG, Edwards MR, Ahmed MKA, Thompson R, Averdunk G, Alps H, Danell B, Henderson CR, Legates J. 1983. Heritability of milk yield and composition at different levels and variability of production. Anim Sci. 36:59–68.

Hinde C. 2005. Negotiation over offspring care?–a positive response to partner-provisioning rate in great tits. Behav Ecol. 17:6–12.

Hinde K, Power ML, Oftedal OT. 2009. Rhesus macaque milk: Magnitude, sources, and consequences of individual variation over lactation. Am J Phys Anthropol. 138:148–157.

Hörnfeldt B, Eklund U. 2008. The effect of food on laying date and clutch-size in Tengmalm's Owl *Aegolius funereus*. Ibis. 132:395–406.

Houslay TM, Wilson AJ. 2017. Avoiding the misuse of BLUP in behavioural ecology. Behav Ecol. 28:948–952.

Huang Ws, Wang HY. 2009. Predation risks and anti-predation parental care behavior: an experimental study in a tropical skink. Ethology. 115:273–279.

Humphries MM, Boutin S. 2000. The determinants of optimal litter size in free-ranging red squirrels. Ecology. 81:2867–2877.

Hurrell JW. 1995. Decadal Trends in the North Atlantic Oscillation: Regional Temperatures and Precipitation. Science. 269:676–679.

Hutchings JA. 1999. Influence of growth and survival costs of reproduction on Atlantic cod, *Gadus morhua*, population growth rate. Can J Fish Aquat Sci. 56:1612–1623.

Hutchings MR, Milner JM, Gordon IJ, Kyriazakis I, Jackson F. 2002. Grazing decisions of Soay sheep, *Ovis aries*, on St Kilda: a consequence of parasite distribution? Oikos. 96:235–244.

Jacquemyn H, Brys R, Jongejans E. 2010. Size-dependent flowering and costs of reproduction affect population dynamics in a tuberous perennial woodland orchid. J Ecol. 98:1204–1215.

Jager HI. 2001. Individual variation in life history characteristics can influence extinction risk. Ecol Model. 144:61–76.

Jeschke JM, Kokko H. 2009. The roles of body size and phylogeny in fast and slow life histories. Evol Ecol. 23:867–878.

Jewell PA. 1974. Island Survivors: Ecology of the Soay Sheep of St. Kilda. London: Athlone Press.

Johannesson B, Johannesson K. 1996. Population differences in behaviour and morphology in the snail *Littorina saxatilis*: phenotypic plasticity or genetic differentiation? J Zool. 240:475–493.

Johnson DH. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology. 61:65–71.

Jones OR. 2003. Grazing ecology, parasitism and performance of Soay sheep on St. Kilda Phd. Imperial College London.

Jones OR, Crawley MJ, Pilkington JG, Pemberton JM. 2005. Predictors of early survival in Soay sheep: cohort-, maternal- and individual-level variation. Proc R Soc Lond B Biol Sci. 272:2619–25.

Jones OR, Pilkington JG, Crawley MJ. 2006. Distribution of a naturally fluctuating ungulate population among heterogeneous plant communities: ideal and free? J Anim Ecol. 75:1387–1392.

Jorgenson JT, Festa-Bianchet M, Lucherini M, Wishart WD. 1993. Effects of body size, population density, and maternal characteristics on age at first reproduction in bighorn ewes. Can J Zool. 71:2509–2517.

Karels TJ, Byrom AE, Boonstra R, Krebs CJ. 2000. The interactive effects of food and predators on reproduction and overwinter survival of arctic ground squirrels. J Anim Ecol. 69:235–247.

Kie JG. 2013. A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. Anim Biotelemetry. 1:13.

Kie JG, Matthiopoulos J, Fieberg J, Powell RA, Cagnacci F, Mitchell MS, Gaillard JM, Moorcroft PR. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? Philos Trans R Soc Lond B Biol Sci. 365:2221–31.

Kilner RM, Hinde C. 2012. Parent-offspring conflict. In: Royle NJ, Smiseth PT, Kölliker M, editors, The Evolution of Parental Care. Oxford, United Kingdom: Oxford University Press. p. 119–129.

Kjellander P, Gaillard J, Hewison M, Liberg O. 2004. Predation risk and longevity influence variation in fitness of female roe deer (*Capreolus capreolus L.*). Proc R Soc London B Biol Sci. 271.

Kjellander P, Gaillard JM, Hewison AJM. 2006. Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. Oecologia. 146:521–530.

Koivula M, Koskela E, Mappes T, Oksanen TA. 2003. Cost of reproduction in the wild: manipulation of reproductive effort in the bank vole. Ecology. 84:398–405.

Kolliker M, Heeb P, Werner I, Mateman AC, Lessells CM, Richner H. 1999. Offspring sex ratio is related to male body size in the great tit (*Parus major*). Behav Ecol. 10:68–72.

Komdeur J. 1996. Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. Behav Ecol. 7:326–333.

Kontiainen P, Pietiäinen H, Huttunen K, Karell P, Kolunen H, Brommer JE. 2009. Aggressive Ural owl mothers recruit more offspring. Behav Ecol. 20:789–796.

Korpimäki E, Hakkarainen H. 1991. Fluctuating food supply affects the clutch size of Tengmalm's owl independent of laying date. Oecologia. 85:543–552.

Kotiaho JS, Simmons LW. 2003. Longevity cost of reproduction for males but no longevity cost of mating or courtship for females in the male-dimorphic dung beetle *Onthophagus binodis*. J Insect Physiol. 49:817–822.

Kruuk LE, Clutton-Brock TH, Rose KE, Guinness FE. 1999. Early determinants of lifetime reproductive success differ between the sexes in red deer. Proc R Soc Lond B Biol Sci. 266:1655–61.

Kruuk LE, Slate J, Wilson AJ. 2008. New answers for old questions: the evolutionary quantitative genetics of wild animal populations. Annu Rev Ecol Evol Syst. 39:525–548.

Kruuk LEB. 2004. Estimating genetic parameters in natural populations using the "animal model". Philos Trans R Soc Lond B Biol Sci. 359:873–890.

Kruuk LEB, Hadfield JD. 2007. How to separate genetic and environmental causes of similarity between relatives. J Evol Biol. 20:1890–1903.

Lambrechts MM, Caro S, Charmantier A, Gross N, Galan MJ, Perret P, Cartan-Son M, Dias PC, Blondel J, Thomas DW. 2004. Habitat quality as a predictor of spatial variation in blue tit reproductive performance: a multi-plot analysis in a heterogeneous landscape. Oecologia. 141:555–561.

Lande R, Kirkpatrick M. 1990. Selection response in traits with maternal inheritance. Genet Res, Camb. 55:189–197.

Landete-Castillejos T, García A, Gómez JA, Molina A, Gallego L. 2003. Subspecies and body size allometry affect milk production and composition, and calf growth in red deer: comparison of *Cervus elaphus hispanicus* and *Cervus elaphus scoticus*. Physiol Biochem Zool. 76:594–602.

Lane JE, McAdam AG, Charmantier A, Humphries MM, Coltman DW, Fletcher Q, Gorrell JC, Boutin S. 2015. Post-weaning parental care increases fitness but is not heritable in North American red squirrels. J Evol Biol. 28:1203–1212.

Lescroël A, Dugger KM, Ballard G, Ainley DG. 2009. Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. J Anim Ecol. 78:798–806.

Lessells C. 2012. Sexual conflict. In: Royle NJ, Smiseth PT, Kölliker M, editors, The Evolution of Parental Care. Oxford, United Kingdom: Oxford University Press. p. 150–170.

Lidgard DC, Boness DJ, Bowen WD, McMillan JI. 2005. State-dependent male mating tactics in the grey seal: the importance of body size. Behav Ecol. 16:541–549.

Limmer B, Becker PH. 2009. Improvement in chick provisioning with parental experience in a seabird. Anim Behav. 77:1095–1101.

Lindström J, Kokko H. 2002. Cohort effects and population dynamics. Ecol Lett. 5:338–344.

Low M, Makan T, Castro I. 2012. Food availability and offspring demand influence sex-specific patterns and repeatability of parental provisioning. Behav Ecol. 23:25–34.

Lunn NJ, Boyd IL, Croxall JP. 1994. Reproductive performance of female antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. J Anim Ecol. 63:827–840.

Lynch M, Walsh B. 1998. Genetics and analysis of quantitative traits. Sinauer, Sunderland.

MacColl AD, Hatchwell BJ. 2003a. Sharing of caring: nestling provisioning behaviour of long-tailed tit, *Aegithalos caudatus*, parents and helpers. Anim Behav. 66:955–964.

MacColl ADC, Hatchwell BJ. 2003b. Heritability of parental effort in a passerine bird. Evolution. 57:2191–2195.

Magnussen S. 1993. Bias in genetic variance estimates due to spatial autocorrelation. Theor Appl Genet. 86:349–55.

Manly B, McDonald L, Thomas DI, McDonald TI, Erickson WP. 2002. Resource selection by animals. 2nd ed. Dordrecht, the Netherlands: Kluwer Academic Publishers.

Markman S, Pinshow B, Wright J. 2002. The manipulation of food resources reveals sex-specific trade-offs between parental self-feeding and offspring care. Proc R Soc Lond B Biol Sci. 269:1931–8.

Marrow P, Mcnamara JM, Houston AI, Stevenson IR, Clutton-Brock TH. 1996. State-Dependent Life History Evolution in Soay Sheep: Dynamic Modelling of Reproductive State-dependent life history evolution in Soay sheep: dynamic modelling of reproductive scheduling. Philos Trans Biol Sci. 351:17–32.

Martin JGA, Festa-Bianchet M. 2010. Bighorn ewes transfer the costs of reproduction to their lambs. Am Nat. 176:414–423.

Martin TE. 1987. Food as a limit on breeding birds: a life-history perspective. Annu Rev Ecol Syst. 18:453–487.

Martínez-Jauregui M, San Miguel-Ayanz A, Mysterud A, Rodríquez-Vigal C, Clutton-Brock TH, Langvatn R, Coulson T. 2009. Are local weather, NDVI and NAO consistent determinants of red deer weight across three contrasting European countries? Glob Chang Biol. 15:1727–1738.

Matthysen E. 2005. Density-dependent dispersal in birds and mammals. Ecography. 28:403–416.

Mauget C, Mauget R, Sempéré A. 1999. Energy expenditure in European roe deer fawns during the suckling period and its relationship with maternal reproductive cost. Can J Zool. 77:389–396.

McAdam AG, Boutin S, Réale D, Berteaux D. 2002. Maternal effects and the potential for evolution in a natural population of animals. Evolution. 56:846–51.

McCleery R, Perrins C, Sheldon B, Charmantier A. 2008. Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. Proc R Soc London B Biol Sci. 275:963–970.

McCleery R, Pettifor R, Armbruster P, Meyer K, Sheldon B, Perrins C. 2004. Components of variance underlying fitness in a natural population of the great tit *Parus major*. Am Nat. 164:E62–E72.

McGaugh SE, Schwanz LE, Bowden RM, Gonzalez JE, Janzen FJ. 2010. Inheritance of nesting behaviour across natural environmental variation in a turtle with temperature-dependent sex determination. Proc R Soc London B Biol Sci. 277:1219–1226.

McLoughlin PD, Boyce MS, Coulson T, Clutton-Brock T. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. Proc R Soc Lond B Biol Sci. 273:1449–1454.

Mcloughlin PD, Gaillard JM, Boyce MS, Bonenfant C, Messier F, Duncan P, Delorme D, Van Moorter B, Saïd S, Klein F. 2007. Lifetime reproductive success and composition of the home range in a large herbivore. Ecology. 88:3192–3201.

McNamara JM, Houston AI. 1996. State-dependent life histories. Nature. 380:215–221.

Millar JS, Derrickson EM, Sharpe STP. 1992. Effects of reproduction on maternal survival and subsequent reproduction in northern*Peromyscus maniculatus*. Can J Zool. 70:1129–1134.

Milner JM, Elston DA, Albon SD. 1999. Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. J Anim Ecol. 68:1235–1247.

Mobaek R, Mysterud A, Egil Loe L, Holand Ø, Austrheim G. 2009. Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach. Oikos. 118:209–218.

Moen J, Andersen R, Illius A. 2006. Living in a seasonal environment. In: Danell K, Bergström R, Duncan P, Pastor J, editors, Large Herbivore Ecology, Ecosystem Dynamics and Conservation. Cambridge, United Kingdom: Cambridge University Press. p. 50–70.

Møller AP, Birkhead TR. 1993. Certainty of paternity covaries with paternal care in birds. Behav Ecol Sociobiol. 33:261–268.

Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT. 2010. Building the bridge between animal movement and population dynamics. Philos Trans R Soc London B Biol Sci. 365.

Morellet N, Bonenfant C, Börger L, Ossi F, Cagnacci F, Heurich M, Kjellander P, Linnell JDC, Nicoloso S, Sustr P, Urbano F, Mysterud A. 2013. Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. J Anim Ecol. 82:1326–1339.

Morrison C, Hero JM. 2003. Geographic variation in life-history characteristics of amphibians: a review. J Anim Ecol. 72:270–279.

Morrissey MB, Wilson AJ. 2009. pedantics: an r package for pedigree-based genetic simulation and pedigree manipulation, characterization and viewing. Mol Ecol Resour. 10:711–719.

Mourier J, Planes S. 2013. Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia. Mol Ecol. 22:201–214.

Moyes K. 2007. Demographic consequences of individual variation. Ph.D. thesis. University of Kent, Canterbury, U.K.

Moyes K, Coulson T, Morgan BJT, Donald A, Morris SJ, Clutton-Brock TH. 2006. Cumulative reproduction and survival costs in female red deer. Oikos. 115:241–252.

Mutzel A, Blom MP, Spagopoulou F, Wright J, Dingemanse NJ, Kempenaers B. 2013. Temporal trade-offs between nestling provisioning and defence against nest predators in blue tits. Anim Behav. 85:1459–1469.

Naef-Daenzer B, Keller LF. 1999. The foraging performance of great and blue tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. J Anim Ecol. 68:708–718.

Nager RG, Monaghan P, Houston DC. 2001. The cost of egg production: increased egg production reduces future fitness in gulls. J Avian Biol. 32:159–166.

Nagy LR, Holmes RT. 2005. Food limits annual fecundity of a migratory songbird: an experimental study. Ecology. 86:675–681.

Nakagawa S, Gillespie DOS, Hatchwell BJ, Burke T. 2007. Predictable males and unpredictable females: sex difference in repeatability of parental care in a wild bird population. J Evol Biol. 20:1674–1681.

Nams VO. 2014. Combining animal movements and behavioural data to detect behavioural states. Ecol Lett. 17:1228–1237.

Newton-Fisher N. 2012. Animal Behaviour Pro (Version 1.0) [Mobile application software]. Retrieved from http://itunes.apple.com.

Ng J, Landeen EL, Logsdon RM, Glor RE. 2013. Correlation between Anolis lizard deqlap phenotype and environmentl variation indicates adaptive divergence of a signal important to sexual selection and species recognition. Evolution. 67:573–582.

Nicolaus M, Michler SPM, Ubels R, van der Velde M, Bouwman KM, Both C, Tinbergen JM. 2012. Local sex ratio affects the cost of reproduction. J Anim Ecol. 81:564–572.

Nilsson J, Svensson M. 1996. Sibling competition affects nestling growth strategies in marsh tits. J Anim Ecol. 65:825–836.

Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proc R Soc Lond B Biol Sci. 271:59–64.

Nussey DH, Coltman DW, Coulson T, Kruuk LEB, Donald A, Morris SJ, Clutton-Brock TH, Pemberton J. 2005. Rapidly declining fine-scale spatial genetic structure in female red deer. Mol Ecol. 14:3395–3405.

Öberg M, Arlt D, Pärt T, Laugen AT, Eggers S, Low M. 2015. Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. Ecol Evol. 5:345–356.

Ockendon N, Leech D, Pearce-Higgins JW. 2013. Climatic effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carry-over effects from wintering grounds. Biol Lett. 9:1–4.

Oftedal O, Power R, Layne D, Tardif S, Power M. 2001. Lactation, maternal behavior and infant growth in common marmoset monkeys (*Callithrix jacchus*): effects of maternal size and litter size. Behav Ecol Sociobiol. 51:17–25.

Oftedal OT. 1984. Body size and reproductive strategy as correlates of milk energy output in lactating mammals. Acta Zool Fenn. 171:183–186.

Olalla-Tárraga MÁ, Rodríguez MÁ, Ángel M. 2007. Energy and interspecific body size patterns of amphibian faunas in Europe and North America: anurans follow Bergmann's rule, urodeles its converse. Glob Ecol Biogeogr. 16:606–617.

Orell M, Rytkönen S, Koivula K, Ronkainen M, Rahiala M. 1996. Brood size manipulations within the natural range did not reveal intragenerational cost of reproduction in the Willow Tit *Parus montanus*. Ibis. 138:630–637.

Owen-Smith N, Fryxell JM, Merrill EH. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. Philos Trans R Soc London B Biol Sci. 365.

Ozgul A, Tuljapurkar S, Benton TG, Pemberton JM, Clutton-Brock TH, Coulson T. 2009. The dynamics of phenotypic change and the shrinking sheep of St. Kilda. Science. 325:464–467.

Papadopoulos NT, Liedo P, Müller HG, Wang JL, Molleman F, Carey JR. 2010. Cost of reproduction in male medflies: The primacy of sexual courting in extreme longevity reduction. J Insect Physiol. 56:283–287.

Paquet M, Covas R, Chastel O, Parenteau C, Doutrelant C. 2013. Maternal Effects in Relation to Helper Presence in the Cooperatively Breeding Sociable Weaver. PLoS One. 8:e59336.

Partridge L, Sibly R, Beverton RJH, Hill WG. 1991. Constraints in the evolution of life histories [and discussion]. Philos Trans R Soc London B Biol Sci. 332:3–13.

Pelletier F, Garant D, Hendry AP. 2009. Eco-evolutionary dynamics. Philos Trans R Soc Lond B Biol Sci. 364:1483–9.

Pettifor RA, Perrins CM, McCleery RH. 1988. Individual optimization of clutch size in great tits. Nature. 336:160–162.

Pfister CA, Stevens FR. 2003. Individual variation and environmental stochasticity: implication for matrix model predictions. Ecology. 84:496–510.

Pilkington JG, Albon SD, Arthur C, Berenos C, Childs D, Christensen L, Clements D, Clutton-Brock TH, Coulson T, Crawley MJ, Damasceno E, Fairlie J, Ellis P, Garnier R, Godsall B, Graham A, Grenfell B, Hayward A, Harrington L, Herman J, Holland R, Johnston S, Kerr L, Klingenberg C, Kruuk L, Mcneilly T, Morrissey M, Murray S, Nussey D, Pemberton JM, Regan C, Scott P, Selman C, Slate J, Stevenson IR, Timmons Z, Watson R, Watt K, Wilson A, Wilson K, Zamoyska R. 2013. St. Kilda Soay sheep: annual report 2013. Tech. rep.

Pioz M, Loison A, Gauthier D, Gibert P, Jullien JM, Artois M, Gilot-Fromont E. 2008. Diseases and reproductive success in a wild mammal: example in the alpine chamois. Oecologia. 155:691–704.

Postma E. 2006. Implications of the difference between true and predicted breeding values for the study of natural selection and micro-evolution. J Evol Biol. 16:309–320.

Powell R. 2000. Animal home ranges and territories and home range estimators. New York, USA: Columbia University Press. p. 65–110.

Powell RA, Mitchell MS. 2012. What is a home range? J Mammal. 93:948–958.

Pradel R. 2005. Multievent: An Extension of Multistate Capture-Recapture Models to Uncertain States. Biometrics. 61:442–447.

Preston BT, Stevenson IR, Pemberton JM, Coltman DW, Wilson K. 2003. Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. Proc R Soc London B Biol Sci. 270:633–640.

Promislow DEL, Harvey PH. 1990. Living fast and dying young: A comparative analysis of life-history variation among mammals. J Zool. 220:417–437.

Pyle P, Spear LB, Sydeman WJ, Ainley DG. 1991. The effects of experience and age on the breeding peformance of western gulls.

Qiao CG, Basford KE, DeLacy IH, Cooper M. 2000. Evaluation of experimental designs and spatial analyses in wheat breeding trials. Theor Appl Genet. 100:9–16.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rachlow JL, Bowyer RT. 1994. Variability in maternal behavior by Dall's sheep: environmental tracking or adaptive strategy? J Mammal. 75:328–337.

Regan CE, Pilkington JG, Bérénos C, Pemberton JM, Smiseth PT, Wilson AJ. 2017a. Accounting for female space sharing in St. Kilda Soay sheep (*Ovis aries*) results in little change in heritability estimates. J Evol Biol. 30:96–111.

Regan CE, Pilkington JG, Pemberton JM, Crawley MJ. 2016. Sex differences in relationships between habitat use and reproductive performance in Soay sheep (*Ovis aries*). Ecol Lett. 19:171–179.

Regan CE, Pilkington JG, Smiseth PT. 2017b. Female Soay sheep do not adjust their maternal care behaviour to the quality of their home range. Behav Ecol. 118:450–459.

Robertson A, Hiraiwa-Hasegawa M, Albon SD, Clutton-Brock TH. 1992. Early growth and sucking behaviour of Soay sheep in a fluctuating population. J Zool. 227:661–672.

Rose KE, Clutton-Brock TH, Guinness FE. 1998. Cohort variation in male survival and lifetime breeding success in red deer. J Anim Ecol. 67:979–986.

Rossiter SJ, Jones G, Ransome RD, Barratt EM. 2002. Relatedness structure and kin-biased foraging in the greater horseshoe bat (*Rhinolophus ferrumequinum*). Behav Ecol Sociobiol. 51:510–518.

Royle NJ, Russell AF, Wilson AJ. 2014. The evolution of flexible parenting. Science. 345:776–781.

Ruckstuhl KE, Festa-Bianchet M. 2010. Do reproductive status and lamb gender affect the foraging behavior of bighorn ewes? Ethology. 104:941–954.

Russell AF, Clutton-Brock TH, Brotherton PNM, Sharpe LL, Mcilrath GM, Dalerum FD, Cameron EZ, Barnard JA. 2002. Factors affecting pup growth and survival in co-operatively breeding meerkats *Suricata suricatta*. J Anim Ecol. 71:700–709.

Russell AF, Langmore NE, Gardner JL, Kilner RM. 2008. Maternal investment tactics in superb fairy-wrens. Proc R Soc Lond B Biol Sci. 275:29–36.

Saether BE, Heim M. 1993. Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. Source J Anim Ecol. 62:482–489.

Saïd S, Gaillard JM, Duncan P, Guillon N, Guillon N, Servanty S, Pellerin M, Lefeuvre K, Martin C, Van Laere G. 2005. Ecological correlates of home-range size in springsummer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. J Zool. 267:301–308.

Saïd S, Gaillard JM, Widmer O, Débias F, Bourgoin G, Delorme D, Roux C. 2009. What shapes intra-specific variation in home range size? A case study of female roe deer. Oikos. 118:1299–1306.

Sand H. 1996. Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. Oecologia. 106:212–220.

Sanz JJ, Tinbergen JM. 1999. Energy expenditure, nestling age, and brood size: an experimental study of parental behavior in the great tit *Parus major*. Behav Ecol. 10:598–606.

Schuett GW. 1997. Body size and agonistic experience affect dominance and mating success in male copperheads. Anim Behav. 54:213–224.

Schulte-Hostedde AI, Zinner B, Millar JS, Hickling GJ. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology. 86:155–163.

Scornavacca D, Lovari S, Cotza A, Bernardini S, Brunetti C, Pietrocini V, Ferretti F. 2016. Pasture quality affects juvenile survival through reduced maternal care in a mountain-dwelling ungulate. Ethology. 122:807–817.

Scott D. 1980. Functional aspects of prolonged parental care in Bewick's swans. Anim Behav. 28:938–952.

Seaman D, Millspaugh J, Kernohan B, Brundige G, Raedeke K, Gitzen R. 1999. Effects of Sample Size on Kernel Home Range Estimates. J Wildl Manag. 63:739–747.

Seki SI, Takano H. 1998. Caterpillar abundance in the territory affects the breeding performance of great tit *Parus major minor*. Oecologia. 114:514–521.

Serrano E, Colom-Cadena A, Gilot-Fromont E, Garel M, Cabezón O, Velarde R, Fernández-Sirera L, Fernández-Aguilar X, Rosell R, Lavín S, Marco I. 2015. Border Disease Virus: An Exceptional Driver of Chamois Populations Among Other Threats. Front Microbiol. 6:1307–1316.

Servanty S, Gaillard JM, Toïgo C, Brandt S, Baubet E. 2009. Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. J Anim Ecol. 78:1278–1290.

Sheridan CM, Spotila JR, Bien WF, Avery HW. 2010. Sex-biased dispersal and natal philopatry in the diamondback terrapin, *Malaclemys terrapin*. Mol Ecol. 19:5497–510.

Sillett TS, Rodenhouse NL, Holmes RT. 2004. Experimentally reducing neighbour density affects reproduction and behavior of a migratory songbird. Ecology. 85:2467–2477.

Silva JCe, Dutkowski GW, Gilmour AR. 2001. Analysis of early tree height in forest genetic trials is enhanced by including a spatially correlated residual. Can J For Res. 31:1887–1893.

Skaug H, Fournier D, Nielsen A. 2006. glmmADMB: Generalized linear mixed models using AD Model Builder. Available: http://glmmadmb.r-forge.r-project.org/.

Skibiel AL, Hood WR. 2015. Milk matters: offspring survival in Columbian ground squirrels is affected by nutrient composition of mother's milk. Front Ecol Evol. 3:111–121.

Slate J, Kruuk LEB, Marshall TC, Pemberton JM, Clutton-Brock TH. 2000. Inbreeding depression influences lifetime breeding success in a wild population of red deer (*Cervus elaphus*). Proc R Soc London B Biol Sci. 267.

Smiseth PT, Kölliker M, Royle NJ. 2012. What is parental care? In: Royle NJ, Smiseth PT, Kölliker M, editors, The Evolution of Parental Care. Oxford, United Kingdom: Oxford University Press. p. 1–14.

Stahlschmidt ZR. 2011. Taxonomic chauvinism revisited: insight from parental care research. PLoS One. 6:e24192.

Stearns SC. 1976. Life-history tactics: a review of the ideas. Q Rev Biol. 51:3–47.

Stearns SC. 1977. The evolution of life history traits: a critique of the theory and a review of the data. Ann Rev Ecol Syst. 8:145–71.

Stearns SC. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. Oikos. 41:173.

Stearns SC. 1989. Trade-Offs in Life-History Evolution. Funct Ecol. 3:259.

Stearns SC. 2000. Life history evolution: Successes, limitations, and prospects. 87:476–486.

Stein AC, Uy JAC. 2005. Plumage brightness predicts male mating success in the lekking golden-collared manakin, *Manacus vitellinus*. Behav Ecol. 17:41–47.

Stopher KV, Walling CA, Morris A, Guinness FE, Clutton-Brock TH, Pemberton JM, Nussey DH. 2012. Shared spatial effects on quantitative genetic parameters: Accounting for spatial autocorrelation and home range overlap reduces estimates of heritability in wild red deer. Evolution. 66:2411–2426.

Sydeman WJ, Huber HR, Emslie SD, Ribic CA, Nur N. 1991. Age-specific weaning success of northern elephant seals in relation to previous breeding experience. Ecology. 72:2204–2217.

Tavecchia G, Coulson T, Morgan BJT, Pemberton JM, Pilkington JG, Gulland F, Clutton-Brock TH. 2005. Predictors of reproductive cost in female Soay sheep. J Anim Ecol. 74:201–213.

Tavecchia G, Pradel R, Boy V, Johnson AR, Cézilly F. 2001. Sex- and age-related variation in survival and cost of first reproduction in greater flamingos. Ecology. 82:165–174.

Teplitsky C, Mills JA, Alho JS, Yarrall JW, Merilä J. 2008. Bergmann's rule and climate change revisited: disentangling environmental and genetic responses in a wild bird population. Proc Natl Acad Sci U S A. 105:13492–6.

Therrien JF, Côté SD, Festa-Bianchet M, Ouellet JP. 2007. Conservative maternal care in an iteroparous mammal: a resource allocation experiment. Behav Ecol Sociobiol. 62:193–199.

Thierry AM, Massemin S, Handrich Y, Raclot T. 2013. Elevated corticosterone levels and severe weather conditions decrease parental investment of incubating Adélie penguins. Horm Behav. 63:475–483.

Thusius KJ, Peterson KA, Dunn PO, Whittingham LA. 2001. Male mask size is correlated with mating success in the common yellowthroat. Anim Behav. 62:435–446.

Toïgo C, Gaillard JM, Van Laere G, Hewison M, Morellet N. 2006. How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. Ecography. 29:301–308.

Tollefson TN, Shipley LA, Myers WL, Dasgupta N. 2011. Forage quality's influence on mule deer fawns. J Wildl Manage. 75:919–928.

Tremblay I, Thomas D, Blondel J, Perret P, Lambrechts MM. 2004. The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits *Parus caeruleus*. Ibis. 147:17–24.

Tschirren B, Sendecka J, Groothuis TGG, Gustafsson L, Doligez B. 2009. Heritable variation in maternal yolk hormone transfer in a wild bird population. Am Nat. 174:557–64.

Tufto J, Andersen R, Linnell J. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. J Anim Ecol. 65:715–724.

van Beest FM, Rivrud IM, Loe LE, Milner JM, Mysterud A. 2011a. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? J Anim Ecol. 80:771–785.

van Beest FM, Rivrud IM, Loe LE, Milner JM, Mysterud A. 2011b. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? J Anim Ecol. 80:771–785.

Van Der Jeugd HP, McCleery R. 2002. Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. J Evol Biol. 15:380–387.

van Noordwijk AJ, de Jong G. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. Am Nat. 128:137–142.

Vangen O, Holm B, Valros A, Lund M. 2005. Genetic variation in sows' maternal behaviour, recorded under field conditions. Livest Prod Sci. 93:63–71.

Vergara P, Fargallo JA, Martínez-Padilla J. 2015. Genetic basis and fitness correlates of dynamic carotenoid-based ornamental coloration in male and female common kestrels *Falco tinnunculus*. J Evol Biol. 28:146–54.

Verhulst S, Perrins CM, Riddington R. 1997. Natal dispersal of great tits in a patchy environment. Ecology. 78:864–872.

Vindenes Y, Langangen Ø. 2015. Individual heterogeneity in life histories and eco-evolutionary dynamics. Ecol Lett. 18:417–432.

Visscher PM. 2006. A note on the asymptotic distribution of likelihood ratio tests to test variance components. Twin Res Hum Genet. 9:490–5.

von Holst D, Hutzelmeyer H, Kaetzke P, Khaschei M, Rödel H, Schrutka H. 2002. Social rank, fecundity and lifetime reproductive success in wild European rabbits (*Oryctolagus cuniculus*). Behav Ecol Sociobiol. 51:245–254.

Waser PM, Thomas Jones W. 1989. Heritability of dispersal in banner-tailed kangaroo rats, *Dipodomys spectabilis*. Anim Behav. 37:987–991.

Wauters LA, Dhondt AA, Dhondt AA. 1995. Lifetime reproductive success and its correlates in female Eurasian red squirrels. Oikos. 72:402.

Wauters LA, Lens L. 1995. Effects of food availability and density on red squirrel (*Sciurus Vulgaris*) reproduction. Ecology. 76:2460–2469.

Weese DJ, Schwartz AK, Bentzen P, Hendry AP, Kinnison MT. 2011. Eco-evolutionary effects on population recovery following catastrophic disturbance. Evol Appl. 4:354–366.

Weigensberg I, Roff DA. 1996. Natural heritabilities: can they be reliably estimated in the laboratory? Evolution. 50:2149.

Weimerskirch H. 1990. The influence of age and experience on breeding performance of the Antarctic fulmar, *Fulmarus glacialoides*. J Anim Ecol. 59:867.

Whittingham LA, Robertson RJ. 1994. Food availability, parental care and male mating success in red-winged blackbirds (*Agelaius phoeniceus*). J Anim Ecol. 63:139–150.

Wiley EM, Ridley AR. 2016. The effects of temperature on offspring provisioning in a cooperative breeder. Anim Behav. 117:187–195.

Wilkin TA, Garant D, Gosler AG, Sheldon BC. 2006. Density effects on life-history traits in a wild population of the great tit *Parus major*: analyses of long-term data with GIS techniques. J Anim Ecol. 75:604–615.

Willham RL. 1972. The role of maternal effects in animal breeding. 3. Biometrical aspects of maternal effects in animals. J Anim Sci. 35:1288–93.

Williams GC. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am Nat. 100:687–690.

Wilson AJ, Coltman DW, Pemberton JM, Overall ADJ, Byrne KA, Kruuk LEB. 2005. Maternal genetic effects set the potential for evolution in a free-living vertebrate population. J Evol Biol. 18:405–14.

Wilson AJ, Morrissey MB, Adams MJ, Walling CA, Guinness FE, Pemberton JM, Clutton-Brock TH, Kruuk LEB. 2011. Indirect genetics effects and evolutionary constraint: an analysis of social dominance in red deer, *Cervus elaphus*. J Evol Biol. 24:772–783.

Wilson AJ, Nussey DH. 2010. What is individual quality? An evolutionary perspective. Trends Ecol Evol. 25:207–214.

Wilson AJ, Pemberton JM, Pilkington JG, Clutton-Brock TH, Coltman DW, Kruuk LEB. 2007. Quantitative genetics of growth and cryptic evolution of body size in an island population. Evol Ecol. 21:337–356.

Wilson AJ, Pemberton JM, Pilkington JG, Clutton-Brock TH, Kruuk LEB. 2009. Trading offspring size for number in a variable environment: selection on reproductive investment in female Soay sheep. J Anim Ecol. 78:354–364.

Wilson AJ, Réale D, Clements MN, Morrissey MM, Postma E, Walling CA, Kruuk LEB, Nussey DH. 2010. An ecologist's guide to the animal model. J Anim Ecol. 79:13–26.

Winkler DW. 1987. A general model for parental care. Am Nat. 130:526–543.

Wolf M, van Doorn GS, Leimar O, Weissing FJ. 2007. Life-history trade-offs favour the evolution of animal personalities. Nature. 447:581–584.

Wong JWY, Kölliker M. 2012. The effect of female condition on maternal care in the European earwig. Ethology. 118:450–459.

Worton B. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology. 70:164–168.

Zhang X, King ML, Hyndman RJ. 2006. A Bayesian approach to bandwidth selection for multivariate kernel density estimation. Comput Stat Data Anal. 50:3009–3031.

Appendix A

Supplementary material for Chapter 2

Table S1: AICc values for the full and best fit models of each female and lamb behavior

Individual	Behavior	Home range quality measure	Full model AICc	Best model AICc
Lamb	Suckling frequency	Lifetime mean % cover of *H. lanatus*	2269.994	2268.057
		Annual mean % cover of *H. lanatus*	2271.834	2268.057
		Annual absolute cover of *H. lanatus*	2270.994	2268.057
		Resource selection function	2334.638	2332.697
Lamb	Total sucking time	Lifetime mean % cover of *H. lanatus*	1981.925	1977.954
		Annual mean % cover of *H. lanatus*	1982.741	1977.954
		Annual absolute cover of *H. lanatus*	1980.825	1977.954
		Resource selection function	1979.552	1977.954
Lamb	Mean suckling duration	Lifetime mean % cover of *H. lanatus*	934.7196	931.2238
		Annual mean % cover of *H. lanatus*	935.6928	931.2238
		Annual absolute cover of *H. lanatus*	936.805	931.2238
		Resource selection function	937.2341	931.2238
Lamb	Suckling success	Lifetime mean % cover of *H. lanatus*	1038.762	1037.527
		Annual mean % cover of *H. lanatus*	1038.322	1037.527
		Annual absolute cover of *H. lanatus*	1039.965	1039.965
		Resource selection function	1027.027	1025.186
Lamb	Grazing time	Lifetime mean % cover of *H. lanatus*	2488.492	2486.042
		Annual mean % cover of *H. lanatus*	2488.494	2486.042
		Annual absolute cover of *H. lanatus*	2490.457	2486.042
		Resource selection function	2493.969	2486.042
Lamb	Resting time	Lifetime mean % cover of *H. lanatus*	9445.035	9444.147
		Annual mean % cover of *H. lanatus*	9444.962	9444.147
		Annual absolute cover of *H. lanatus*	9449.685	9444.147
		Resource selection function	9446.862	9444.147
Female	Grazing frequency	Lifetime mean % cover of *H. lanatus*	4097.776	4094.440
		Annual mean % cover of *H. lanatus*	4097.776	4094.440
		Annual absolute cover of *H. lanatus*	4101.356	4094.440
		Resource selection function	4102.901	4094.44
Female	Resting frequency	Lifetime mean % cover of *H. lanatus*	2764.496	2762.920
		Annual mean % cover of *H. lanatus*	2764.496	2762.920
		Annual absolute cover of *H. lanatus*	2765.576	2762.920
		Resource selection function	2769.141	2762.920
Female	Moving frequency	Lifetime mean % cover of *H. lanatus*	1348.418	1342.896
		Annual mean % cover of *H. lanatus*	1348.418	1342.896
		Annual absolute cover of *H. lanatus*	1346.25	1342.896
		Resource selection function	1346.281	1341.819

Table S2: Parameter estimates (± standard error) for full and best models for all lamb behaviors, using annual home range quality estimates, and including the number of females with overlapping home ranges as an additional fixed effect

Trait	Term	Annual mean % cover of *H. lanatus*				Annual absolute cover of *H. lanatus*			
		Full model		Best model		Full model		Best model	
		Est (SE)	t/z*	Est (SE)	t/z*	Est (SE)	t/z*	Est (SE)	t/z*
Suckling frequency	Lamb age (days)	-1.09(0.06)	-19.73	-1.09(0.06)	-19.76	-1.09(0.06)	-19.73	-1.09(0.06)	-19.76
	Year (2015)	0.39(0.69)	0.57	0.34(0.10)	3.56	0.80(0.80)	1.00	0.34(0.10)	3.56
	Maternal age	-0.02(0.03)	-0.80	-0.04(0.03)	-1.25	-0.05(0.03)	-1.66	-0.04(0.03)	-1.25
	Lamb age^2	0.34(0.06)	5.34	0.35(0.06)	5.36	0.34(0.06)	5.33	0.35(0.06)	5.36
	HR quality	0.06(0.06)	0.96	-	-	-0.04(0.07)	-0.58	-	-
	HR quality^2	0.07(0.05)	1.40	-	-	-0.02(0.03)	-0.63	-	-
	Lamb age:HR quality	-0.02(0.05)	-0.38	-	-	0.05(0.05)	1.15	-	-
	No. overlapping females	0.02(0.34)	0.07	-	-	0.21(0.39)	0.54	-	-
Mean suckle duration	Lamb age (days)	-0.35(0.05)	-7.08	-0.35(0.05)	-7.16	-0.35(0.05)	-7.20	-0.35(0.05)	-7.16
	Year (2015)	-0.41(0.55)	-0.73	-0.03(0.08)	-0.35	-0.78(0.66)	-1.18	-0.03(0.08)	-0.35
	Maternal age	0.02(0.03)	0.89	0.03(0.02)	1.11	0.04(0.03)	1.45	0.03(0.02)	1.11
	Lamb age^2	0.27(0.06)	4.58	0.26(0.06)	4.54	0.27(0.06)	4.58	0.26(0.06)	4.54
	HR quality	-0.05(0.05)	-0.99	-	-	0.07(0.05)	1.24	-	-
	HR quality^2	-0.008(0.04)	-0.21	-	-	-0.01(0.03)	-0.43	-	-
	Lamb age:HR quality	-0.04(0.04)	-1.18	-	-	-0.002(0.04)	-0.06	-	-
	No. overlapping females	-0.20 (0.27)	-0.72	-	-	-0.35(0.32)	-1.11	-	-
Sucking time	Lamb age (days)	-1.41(0.08)	-17.66	-1.41(0.08)	-17.75	-1.42(0.08)	-17.88	-1.41(0.08)	-17.75
	Year (2015)	0.15(0.95)	0.16	0.36(0.13)	2.76	-0.30(1.13)	-0.26	0.36(0.13)	2.76
	Maternal age	0.01(0.04)	0.23	$6.6\times e^{-4}$(0.04)	-0.02	0.004(0.04)	0.08	$6.6\times e^{-4}$(0.04)	-0.02
	Lamb age^2	0.49(0.09)	5.67	0.49(0.09)	5.74	0.51(0.09)	5.91	0.49(0.09)	5.74
	HR quality	0.04(0.08)	0.47	-	-	0.06(0.09)	0.68	-	-
	HR quality^2	0.08(0.07)	1.13	-	-	-0.03(0.05)	-0.70	-	-
	Lamb age:HR quality	-0.02(0.06)	-0.39	-	-	0.10(0.06)	1.75	-	-
	No. overlapping females	-0.12(0.47)	-0.26	-	-	-0.31(0.55)	-0.57	-	-
Suckling success	Lamb age (days)	-0.07(0.11)	-0.68	-0.10(0.11)	-0.96	-0.12(0.11)	-1.15	-0.10(0.11)	-0.96
	Year (2015)	-1.42(1.10)	-1.29	-0.17(0.17)	-1.04	-2.31(1.27)	-1.82	-0.17(0.17)	-1.04
	Maternal age	0.07(0.05)	1.59	0.08(0.04)	1.74	0.10(0.05)	2.11	0.08(0.04)	1.74
	Lamb age^2	0.41(0.13)	3.11	0.39(0.13)	2.98	0.41(0.13)	3.13	0.39(0.13)	2.98

	HR quality	-0.16(0.11)	-1.46	-	-	0.22(0.11)	1.93	-	-
	HR quality^2	-0.08(0.08)	-1.06	-	-	-0.09(0.05)	-1.84	-	-
	Lamb age:HR quality	-0.20(0.10)	-2.00	-	-	0.06(0.10)	0.60	-	-
	No. overlapping females	-0.60(0.55)	-1.09	-	-	-1.00(0.61)	-1.63	-	-
Grazing time	Lamb age (days)	2.85(0.13)	21.79	2.86(0.13)	21.84	2.85(0.13)	21.79	2.86(0.13)	21.84
	Year (2015)	0.55(1.58)	0.35	-0.04(0.23)	-0.19	0.07(1.87)	0.04	-0.04(0.23)	-0.19
	Maternal age	-0.007(0.07)	-0.09	-0.004(0.07)	-0.06	-0.007(0.07)	-0.10	-0.004(0.07)	-0.06
	Lamb age^2	-1.65(0.14)	-11.69	-1.66(0.14)	-11.79	-1.65(0.14)	-11.66	-1.66(0.14)	-11.79
	HR quality	0.06(0.14)	0.43	-	-	0.10(0.15)	0.69	-	-
	HR quality^2	-0.11(0.12)	-0.93	-	-	-0.09(0.90)	-1.25	-	-
	Lamb age:HR quality	0.13(0.09)	1.51	-	-	0.04(0.09)	0.46	-	-
	No. overlapping females	0.37(0.79)	0.47	-	-	0.09(0.90)	0.10	-	-
Resting time	Lamb age (days)	-326.47(58.04)	-5.63	-332.29(57.97)	-5.73	-330.13(58.07)	-5.69	-332.29(57.97)	-5.73
	Year (2015)	125.86(601.88)	0.21	-80.95(88.02)	-0.92	467.31(734.19)	0.64	-80.95(88.02)	-0.92
	Maternal age	17.16(28.07)	0.61	12.10(27.61)	0.44	6.21(28.89)	0.22	12.10(27.61)	0.44
	Lamb age^2	143.91(62.58)	2.30	150.88(62.51)	2.41	147.58(62.84)	2.35	150.88(62.51)	2.41
	HR quality	-3.84(52.67)	-0.07	-	-	-58.17(59.82)	-0.97	-	-
	HR quality^2	87.54(44.32)	1.98	-	-	21.78(29.76)	0.73	-	-
	Lamb age:HR quality	-28.83(40.70)	-0.71	-	-	2.70(40.09)	0.07	-	-
	No. overlapping females	64.62(300.56)	0.22	-	-	255.512(353.51)	0.72	-	-
Female grazing frequency	Lamb age (days)	-0.14(0.02)	-5.78	-0.14(0.02)	-7.96	-0.13(0.02)	-5.63	-0.14(0.02)	-7.96
	Year (2015)	0.02(0.25)	0.10	0.06(0.03)	1.74	0.23(0.29)	0.77	0.06(0.03)	1.74
	Maternal age	0.002(0.01)	0.14	0.005(0.01)	0.48	0.001(0.01)	0.13	0.005(0.01)	0.48
	Lamb age^2	-0.003(0.03)	-0.11	-	-	-0.005(0.03)	-0.20	-	-
	HR quality	-0.02(0.02)	-0.85	-	-	-0.02(0.02)	-0.93	-	-
	HR quality^2	-0.01(0.02)	-0.57	-	-	$7.2\times e^{-4}$(0.01)	0.06	-	-
	Lamb age:HR quality	0.03(0.02)	1.83	-	-	0.01(0.02)	0.68	-	-
	No. overlapping females	-0.02(0.12)	-0.18	-	-	0.08(0.14)	0.53	-	-
Female resting frequency	Lamb age (days)	0.63(0.12)	5.03	0.48(0.08)	5.79	0.60(0.12)	4.88	0.48(0.08)	5.79
	Year (2015)	0.19(1.16)	0.16	-0.43(0.17)	-2.57	-1.28(1.40)	-0.91	-0.43(0.17)	-2.57
	Maternal age	0.01(0.06)	0.24	-0.009(0.05)	-0.17	0.01(0.06)	0.18	-0.009(0.05)	-0.17
	Lamb age^2	-0.17(0.13)	-1.33	-	-	-0.15(0.13)	-1.12	-	-
	HR quality	0.16(0.11)	1.38	-	-	0.18(0.12)	1.52	-	-

	HR quality^2	0.01(0.09)	0.14	-	-	-0.04(0.06)	-0.65	-	-
	Lamb age:HR quality	-0.13(0.08)	-1.58	-	-	-0.03(0.08)	-0.43	-	-
	No. overlapping females	0.36(0.59)	0.62	-	-	-0.37(0.68)	-0.55	-	-
Female moving frequency	Lamb age (days)	0.09(0.09)	0.99	0.11(0.06)	1.73	0.09(0.09)	1.02	0.11(0.06)	1.72
	Year (2015)	-1.40(1.13)	-1.24	0.43(0.17)	2.48	-2.19(1.36)	-1.61	0.37(0.17)	2.12
	Maternal age	-0.04(0.05)	-0.76	-0.02(0.05)	-0.47	-0.01(0.05)	-0.19	-0.03(0.05)	-0.66
	Lamb age^2	0.01(0.10)	0.10	-	-	0.02(0.10)	0.18	-	-
	HR quality	-0.10(0.10)	-1.02	-	-	0.23(0.12)	1.90	0.11(0.10)	1.08
	HR quality^2	-0.17(0.09)	-1.98	-	-	-0.15(0.06)	-2.52	-0.14(0.06)	-2.36
	Lamb age:HR quality	0.08(0.07)	1.25	-	-	0.01(0.07)	0.18	-	-
	No. overlapping females	-0.88(0.56)	-1.57	-	-	-1.24(0.65)	-1.90	-	-

* t values are reported for linear mixed effects models whilst z values are reported for generalised linear mixed effects models.

Table S3: Parameter estimates (± standard error) for full and best models for all lamb behaviors (with and without failed suckling events), using lifetime home range mean percentage cover of *H. lanatus*, annual home range mean percentage cover of *H. lanatus*, and annual resource selection function coefficients

Trait	Term	Lifetime home range				Annual home range				Resource selection function			
		Full model		Best model		Full model		Best model		Full model		Best model	
		Est (SE)	t/z*	Est (SE)	t/z*	Est (SE)	t/z*	Est (SE)	t/z*	Est (SE)	t/z*	Est (SE)	t/z*
Suckling	Lamb age (days)	-1.09(0.06)	-19.81	-1.09(0.06)	-19.76	-1.09(0.06)	-19.73	-1.09(0.06)	-19.76	-1.01(0.07)	-14.08	-1.01(0.06)	-17.06
frequency	Year (2015)	0.33(0.10)	3.21	0.34(0.10)	3.56	0.34(0.10)	3.32	0.34(0.10)	$3.7\times e^{-4}$	0.25(0.11)	2.26	0.31(0.11)	2.83
	Maternal age	-0.02(0.03)	-0.70	-0.04(0.03)	-1.25	-0.02(0.03)	-0.80	-0.04(0.03)	-1.25	-0.03(0.03)	-0.87	-0.04(0.03)	-1.26
	Lamb age^2	0.34(0.06)	5.40	0.35(0.06)	5.36	0.34(0.06)	5.34	0.35(0.06)	5.36	0.34(0.06)	5.29	0.34(0.07)	5.20
	HR quality	0.10(0.06)	1.52	-	-	0.06(0.06)	0.97	-	-	-	-	-	-
	HR quality^2	0.10(0.05)	1.89	-	-	0.07(0.05)	1.40	-	-	-	-	-	-
	Lamb age:HR quality	-0.02(0.05)	-0.38	-	-	-0.02(0.05)	-0.38	-	-	-	-	-	-
	PC1	-	-	-	-	-	-	-	-	-0.02(0.04)	-0.46	-	-
	PC2	-	-	-	-	-	-	-	-	-0.02(0.07)	-0.25	-	-
	PC3	-	-	-	-	-	-	-	-	0.03(0.09)	0.31	-	-
	Lamb age:PC1	-	-	-	-	-	-	-	-	-0.08(0.03)	-2.48	-	-
	Lamb age:PC2	-	-	-	-	-	-	-	-	0.05(0.06)	0.94	-	-
	Lamb age:PC3	-	-	-	-	-	-	-	-	-0.17(0.07)	-2.53	-	-
Mean	Lamb age (days)	-0.35(0.05)	-7.09	-0.35(0.05)	-7.16	-0.35(0.05)	-7.07	-0.35(0.05)	-7.16	-0.36(0.06)	-6.36	-0.35(0.05)	-7.16
suckle	Year (2015)	-0.004(0.09)	-0.05	-0.03(0.08)	-0.35	-0.01(0.09)	-0.15	-0.03(0.08)	-0.35	-0.03(0.09)	-0.34	-0.03(0.08)	-0.35
duration	Maternal age	0.02(0.02)	0.78	0.03(0.02)	1.11	0.02(0.03)	0.89	0.03(0.02)	1.11	0.02(0.02)	0.62	0.03(0.02)	1.11
	Lamb age^2	0.27(0.06)	4.60	0.26(0.06)	4.54	0.27(0.06)	4.55	0.26(0.06)	4.54	0.28(0.06)	4.74	0.26(0.06)	4.54
	HR quality	-0.06(0.05)	-1.33	-	-	-0.04(0.05)	-0.84	-	-	-	-	-	-
	HR quality^2	-0.03(0.04)	-0.60	-	-	-0.007(0.04)	-0.17	-	-	-	-	-	-
	Lamb age:HR quality	-0.04(0.04)	-1.17	-	-	-0.04(0.04)	-1.17	-	-	-	-	-	-
	PC1	-	-	-	-	-	-	-	-	0.03(0.03)	1.10	-	-
	PC2	-	-	-	-	-	-	-	-	$-7.5\times e^{-4}$(0.05)	-0.02	-	-
	PC3	-	-	-	-	-	-	-	-	0.001(0.06)	0.02	-	-
	Lamb age:PC1	-	-	-	-	-	-	-	-	0.04(0.02)	1.73	-	-
	Lamb age:PC2	-	-	-	-	-	-	-	-	0.02(0.04)	0.54	-	-
	Lamb age:PC3	-	-	-	-	-	-	-	-	0.03(0.05)	0.61	-	-
Sucking	Lamb age (days)	-1.41(0.08)	-17.67	-1.41(0.08)	-17.75	-1.41(0.08)	-17.65	-1.41(0.08)	-17.75	-1.48(0.10)	-15.52	-1.43(0.08)	-17.55
time	Year (2015)	0.39(0.14)	2.67	0.36(0.13)	2.76	0.40(0.15)	2.70	0.36(0.13)	2.76	0.36(0.14)	2.58	0.38(0.13)	2.86

	Maternal age	0.01(0.04)	0.27	-6.6×e^{-4}(0.04)	-0.02	0.01(0.04)	0.23	-6.6×e^{-4}(0.04)	-0.02	0.006(0.04)	0.13	0.003(0.04)	0.07
	Lamb age^2	0.49(0.09)	5.69	0.49(0.09)	5.74	0.49(0.09)	5.67	0.49(0.09)	5.74	0.50(0.09)	5.88	0.51(0.09)	5.81
	HR quality	0.07(0.09)	0.82	-	-	0.04(0.08)	0.55	-	-	-	-	-	-
	HR quality^2	0.11(0.07)	1.48	-	-	0.08(0.07)	1.15	-	-	-	-	-	-
	Lamb age:HR quality	-0.02(0.06)	-0.40	-	-	-0.02(0.06)	-0.38	-	-	-	-	-	-
	PC1	-	-	-	-	-	-	-	-	-0.01(0.05)	-0.27	-	-
	PC2	-	-	-	-	-	-	-	-	-0.09(0.09)	-1.03	-	-
	PC3	-	-	-	-	-	-	-	-	0.07(0.11)	0.66	-	-
	Lamb age:PC1	-	-	-	-	-	-	-	-	-0.09(0.04)	-2.30	-	-
	Lamb age:PC2	-	-	-	-	-	-	-	-	0.16(0.07)	2.23	-	-
	Lamb age:PC3	-	-	-	-	-	-	-	-	-0.27(0.09)	-3.06	-	-
Suckling	Lamb age (days)	-0.07(0.11)	-0.62	-0.10(0.11)	-0.96	-0.07(0.11)	-0.67	-0.10(0.11)	-0.96	-0.05(0.13)	-0.38	-0.005(0.12)	-0.04
success	Year (2015)	-0.20(0.18)	-1.12	-0.17(0.17)	-1.04	-0.24(0.18)	-1.32	-0.17(0.17)	-1.04	-0.10(0.17)	-0.56	-0.11(0.17)	-0.67
	Maternal age	0.07(0.11)	1.62	0.08(0.04)	1.74	0.07(0.05)	1.60	0.08(0.04)	1.74	0.10(0.05)	2.02	0.09(0.05)	1.93
	Lamb age^2	0.41(0.13)	3.12	0.39(0.13)	2.98	0.41(0.13)	3.10	0.39(0.13)	2.98	0.48(0.14)	3.52	0.49(0.13)	3.63
	HR quality	-0.15(0.11)	-1.41	-	-	-0.13(0.11)	-1.25	-	-	-	-	-	-
	HR quality^2	-0.07(0.08)	-0.84	-	-	-0.08(0.08)	-1.05	-	-	-	-	-	-
	Lamb age:HR quality	-0.20(0.10)	-1.99	-	-	-0.20(0.10)	-1.99	-	-	-	-	-	-
	PC1	-	-	-	-	-	-	-	-	0.003(0.07)	0.04	0.002(0.06)	0.04
	PC2	-	-	-	-	-	-	-	-	0.19(0.12)	1.51	-	-
	PC3	-	-	-	-	-	-	-	-	-0.21(0.14)	-1.49	-0.06(0.10)	-0.61
	Lamb age:PC1	-	-	-	-	-	-	-	-	0.26(0.07)	3.94	0.24(0.06)	3.79
	Lamb age:PC2	-	-	-	-	-	-	-	-	0.12(0.13)	0.96	-	-
	Lamb age:PC3	-	-	-	-	-	-	-	-	0.18(0.13)	1.40	0.26(0.09)	2.80
Grazing	Lamb age (days)	2.85(0.13)	21.82	2.86(0.13)	21.84	2.85(0.13)	21.79	2.86(0.12)	21.84	2.83(0.16)	18.06	2.86(0.13)	21.84
time	Year (2015)	-0.16(0.25)	-0.63	-0.04(0.23)	-0.19	-0.17(0.25)	-0.68	-0.04(0.23)	-0.19	-0.14(0.25)	-0.58	-0.04(0.223)	-0.19
	Maternal age	-0.003(0.07)	-0.047	-0.004(0.07)	-0.06	-0.007(0.07)	-0.10	-0.004(0.07)	-0.06	0.01(0.07)	0.14	-0.004(0.07)	-0.06
	Lamb age^2	-1.65(0.14)	-11.73	-1.66(0.14)	-11.79	-1.65(0.14)	-11.69	-1.66(0.14)	-11.79	-1.66(0.14)	-11.59	-1.66(0.14)	-11.79
	HR quality	0.05(0.14)	0.33	-	-	0.04(0.13)	0.32	-	-	-	-	-	-
	HR quality^2	-0.10(0.12)	-0.83	-	-	-0.11(0.12)	-0.96	-	-	-	-	-	-
	Lamb age:HR quality	0.14(0.09)	1.54	-	-	0.13(0.09)	1.50	-	-	-	-	-	-
	PC1	-	-	-	-	-	-	-	-	0.05(0.08)	0.63	-	-
	PC2	-	-	-	-	-	-	-	-	-0.07(0.14)	-0.48	-	-
	PC3	-	-	-	-	-	-	-	-	0.20(0.19)	1.08	-	-
	Lamb age:PC1	-	-	-	-	-	-	-	-	-0.10(0.06)	-1.58	-	-

	Lamb age:PC2	-	-	-	-	-	-	-	-	0.10(0.11)	0.86	-	-
	Lamb age:PC3	-	-	-	-	-	-	-	-	-0.22(0.14)	-1.60	-	-
Resting	Lamb age (days)	-328.46(58.03)	-5.66	-332.29(57.97)	-5.73	-326.49(58.05)	-5.62	-332.29(57.97)	-5.73	-367.51(69.51)	-5.29	-332.29(57.97)	-5.73
time	Year (2015)	-3.97(95.43)	-0.04	-80.95(88.02)	-0.92	-1.87(95.86)	-0.02	-80.95(88.02)	-0.92	-109.28(93.71)	-1.17	-80.95(88.02)	-0.92
	Maternal age	12.67(28.00)	0.45	12.10(27.61)	0.44	17.06(28.11)	0.61	12.10(27.61)	0.44	5.05(28.46)	0.18	12.10(27.61)	0.44
	Lamb age^2	146.43(62.54)	2.34	150.88(62.51)	2.41	143.71(62.59)	2.30	150.88(62.51)	2.41	150.75(62.69)	2.41	150.88(62.51)	2.41
	HR quality	-19.35(54.49)	-0.36	-	-	-6.78(51.25)	-0.13	-	-	-	-	-	-
	HR quality^2	80.72(47.70)	1.69	-	-	86.94(44.29)	1.96	-	-	-	-	-	-
	Lamb age:HR quality	-29.24(40.77)	-0.72	-	-	-29.02(40.69)	-0.71	-	-	-	-	-	-
	PC1	-	-	-	-	-	-	-	-	42.69(32.88)	1.30	-	-
	PC2	-	-	-	-	-	-	-	-	2.05(55.92)	0.04	-	-
	PC3	-	-	-	-	-	-	-	-	45.22(72.01)	0.63	-	-
	Lamb age:PC1	-	-	-	-	-	-	-	-	75.23(29.46)	2.55	-	-
	Lamb age:PC2	-	-	-	-	-	-	-	-	27.58(52.18)	0.53	-	-
	Lamb age:PC3	-	-	-	-	-	-	-	-	93.27(63.63)	1.47	-	-
Suckling	Lamb age (days)	-1.15(0.05)	-21.09	-1.16(0.05)	-21.22	-1.15(0.05)	-21.12	-1.16(0.05)	-21.22	-1.13(0.07)	-15.64	-1.13(0.06)	-20.20
frequency	Year (2015)	0.23(0.13)	1.76	0.25(0.12)	2.08	0.24(0.13)	1.79	0.25(0.12)	2.08	0.23(0.11)	2.02	0.25(0.11)	2.41
(only	Maternal age	-0.01(0.04)	-0.29	-0.03(0.04)	-0.71	-0.01(0.04)	-0.35	-0.03(0.04)	-0.71	-0.007(0.04)	-0.20	-0.02(0.03)	0.56
successful)	Lamb age^2	0.50(0.06)	7.77	0.50(0.06)	7.84	0.49(0.06)	7.76	0.50(0.06)	7.84	0.47(0.07)	7.22	0.47(0.07)	7.27
	HR quality	0.06(0.08)	0.75	-	-	0.03(0.07)	0.43	-	-	-	-	-	-
	HR quality^2	0.07(0.06)	1.16	-	-	0.05(0.06)	0.76	-	-	-	-	-	-
	Lamb age:HR quality	-0.05(0.04)	-1.16	-	-	-0.06(0.04)	-1.26	-	-	-	-	-	-
	PC1	-	-	-	-	-	-	-	-	-0.02(0.04)	-0.51	-	-
	PC2	-	-	-	-	-	-	-	-	0.01(0.08)	0.15	-	-
	PC3	-	-	-	-	-	-	-	-	-0.02(0.10)	-0.20	-	-
	Lamb age:PC1	-	-	-	-	-	-	-	-	-0.03(0.03)	-0.98	-	-
	Lamb age:PC2	-	-	-	-	-	-	-	-	0.07(0.06)	1.14	-	-
	Lamb age:PC3	-	-	-	-	-	-	-	-	-0.13(0.07)	-1.82	-	-
Mean	Lamb age (days)	-0.29(0.04)	-6.43	-0.29(0.04)	-6.44	-0.29(0.04)	-6.42	-0.29(0.04)	-6.44	-0.28(0.05)	-5.51	-0.29(0.04)	-6.44
suckle	Year (2015)	-0.05(0.09)	-0.50	-0.05(0.09)	-0.57	-0.06(0.09)	-0.64	-0.05(0.09)	1.10	-0.04(0.09)	-0.47	-0.05(0.09)	-0.57
duration	Maternal age	0.02(0.03)	0.93	0.03(0.02)	1.10	0.03(0.03)	1.02	0.03(0.02)	1.10	0.02(0.03)	0.67	0.03(0.02)	1.10
(only	Lamb age^2	0.28(0.05)	5.35	0.28(0.05)	5.34	0.28(0.05)	5.33	0.28(0.05)	5.34	0.29(0.05)	5.47	0.28(0.05)	5.34
successful)	HR quality	-0.02(0.05)	-0.49	-	-	-0.003(0.05)	-0.07	-	-	-	-	-	-
	HR quality^2	-0.02(0.04)	-0.54	-	-	-0.01(0.04)	-0.34	-	-	-	-	-	-
	Lamb age:HR quality	-0.003(0.03)	-0.09	-	-	-0.006(0.03)	-0.18	-	-	-	-	-	-

	PC1	-	-	-	-	-	-	-	-	0.02(0.03)	0.57	-	-
	PC2	-	-	-	-	-	-	-	-	-0.02(0.05)	-0.39	-	-
	PC3	-	-	-	-	-	-	-	-	$5.7\times e^{-4}$(0.06)	0.009	-	-
	Lamb age:PC1	-	-	-	-	-	-	-	-	0.02(0.02)	1.03	-	-
	Lamb age:PC2	-	-	-	-	-	-	-	-	-0.004(0.04)	-0.11	-	-
	Lamb age:PC3	-	-	-	-	-	-	-	-	0.03(0.05)	0.59	-	-
Sucking	Lamb age (days)	-1.43(0.08)	-17.46	-1.43(0.08)	-17.55	-1.43(0.08)	-17.44	-1.43(0.08)	-17.55	-1.50(0.10)	-15.31	-1.43(0.08)	-17.55
time	Year (2015)	0.41(0.15)	2.80	0.38(0.13)	2.86	0.42(0.15)	2.83	0.38(0.13)	2.86	0.39(0.14)	2.72	0.38(0.13)	2.86
(only	Maternal age	0.01(0.04)	0.28	0.003(0.04)	0.07	0.01(0.04)	0.26	0.003(0.04)	0.07	0.005(0.04)	0.12	0.003(0.04)	0.07
successful)	Lamb age^2	0.51(0.09)	5.74	0.51(0.09)	5.81	0.50(0.09)	5.72	0.51(0.09)	5.81	0.52(0.09)	5.94	0.51(0.09)	5.81
	HR quality	0.04(0.09)	0.51	-	-	0.03(0.08)	0.31	-	-	-	-	-	-
	HR quality^2	0.09(0.08)	1.20	-	-	0.07(0.07)	1.00	-	-	-	-	-	-
	Lamb age:HR quality	-0.05(0.06)	-0.84	-	-	-0.05(0.06)	-0.83	-	-	-	-	-	-
	PC1	-	-	-	-	-	-	-	-	-0.01(0.05)	-0.23	-	-
	PC2	-	-	-	-	-	-	-	-	-0.06(0.09)	-0.73	-	-
	PC3	-	-	-	-	-	-	-	-	0.04(0.11)	0.36	-	-
	Lamb age:PC1	-	-	-	-	-	-	-	-	-0.08(0.04)	-1.79	-	-
	Lamb age:PC2	-	-	-	-	-	-	-	-	0.18(0.07)	2.37	-	-
	Lamb age:PC3	-	-	-	-	-	-	-	-	-0.27(0.09)	-2.95	-	-

* t values are reported for linear mixed effects models whilst z values are reported for generalised linear mixed effects models.

Table S4: Parameter estimates (± standard error) for full and best models for all female behaviors, using lifetime home range quality estimates, annual mean % cover of *H. lanatus*, and annual resource selection function coefficients

Trait	Term	Lifetime home range				Annual home range				Resource selection function			
		Full model		Best model		Full model		Best model		Full model		Best model	
		Est (SE)	z	Est (SE)	z	Est (SE)	z	Est (SE)	z	Est (SE)	z	Est (SE)	z
Grazing frequency	Lamb age (days)	-0.13(0.02)	-5.78	-0.14(0.02)	-7.96	-0.13(0.02)	-5.78	-0.14(0.02)	-7.96	-0.12(0.03)	-4.26	-0.14(0.02)	-7.96
	Year (2015)	0.07(0.04)	1.75	0.06(0.03)	1.74	0.07(0.04)	1.75	0.06(0.03)	1.74	0.06(0.04)	1.76	0.06(0.03)	1.74
	Maternal age	0.002(0.01)	0.20	0.005(0.01)	0.48	0.002(0.01)	0.20	0.005(0.01)	0.48	0.008(0.01)	0.70	0.005(0.01)	0.48
	Lamb age^2	-0.003(0.03)	-0.13	-	-	-0.003(0.03)	-0.13	-	-	-0.006(0.03)	-0.25	-	-
	HR quality	-0.01(0.02)	-0.62	-	-	-0.01(0.02)	-0.62	-	-	-	-	-	-
	HR quality^2	-0.01(0.02)	-0.58	-	-	-0.01(0.02)	-0.58	-	-	-	-	-	-
	Lamb age:HR quality	0.04(0.02)	2.10	-	-	0.04(0.02)	2.10	-	-	-	-	-	-
	PC1	-	-	-	-	-	-	-	-	-0.01(0.01)	-0.79	-	-
	PC2	-	-	-	-	-	-	-	-	0.005(0.02)	0.23	-	-
	PC3	-	-	-	-	-	-	-	-	-0.01(0.03)	-0.48	-	-
	Lamb age:PC1	-	-	-	-	-	-	-	-	-0.02(0.01)	-1.76	-	-
	Lamb age:PC2	-	-	-	-	-	-	-	-	-0.03(0.02)	-1.36	-	-
	Lamb age:PC3	-	-	-	-	-	-	-	-	$8.1\times e^{-4}$(0.03)	0.03	-	-
Resting frequency	Lamb age (days)	0.64(0.12)	5.17	0.48(0.08)	5.79	0.64(0.12)	5.17	0.48(0.08)	5.79	0.53(0.14)	3.69	0.48(0.08)	5.79
	Year (2015)	-0.53(0.19)	-2.76	-0.43(0.17)	-2.57	-0.53(0.19)	-2.76	-0.43(0.17)	-2.57	-0.35(0.18)	-1.92	-0.43(0.17)	-2.57
	Maternal age	0.01(0.06)	0.27	-0.009(0.05)	-0.17	0.01(0.06)	0.27	-0.009(0.05)	-0.17	-0.01(0.06)	-0.21	-0.009(0.05)	-0.17
	Lamb age^2	-0.18(0.13)	-1.43	-	-	-0.18(0.13)	-1.43	-	-	-0.15(0.13)	-1.16	-	-
	HR quality	0.17(0.11)	1.51	-	-	0.17(0.11)	1.51	-	-	-	-	-	-
	HR quality^2	0.05(0.09)	0.49	-	-	0.05(0.09)	0.49	-	-	-	-	-	-
	Lamb age:HR quality	-0.15(0.08)	-1.78	-	-	-0.15(0.08)	-1.78	-	-	-	-	-	-
	PC1	-	-	-	-	-	-	-	-	-0.05(0.07)	-0.72	-	-
	PC2	-	-	-	-	-	-	-	-	-0.09(0.11)	-0.80	-	-
	PC3	-	-	-	-	-	-	-	-	0.001(0.14)	0.01	-	-
	Lamb age:PC1	-	-	-	-	-	-	-	-	0.14(0.06)	2.26	-	-
	Lamb age:PC2	-	-	-	-	-	-	-	-	0.11(0.11)	1.03	-	-
	Lamb age:PC3	-	-	-	-	-	-	-	-	0.09(0.13)	0.67	-	-
Moving frequency	Lamb age (days)	0.09(0.09)	1.01	0.11(0.06)	1.73	0.09(0.09)	1.01	0.11(0.06)	1.73	0.20(0.11)	1.86	0.20(0.09)	2.34
	Year (2015)	0.39(0.19)	2.04	0.43(0.17)	2.48	0.39(0.19)	2.04	0.43(0.17)	2.48	0.51(0.18)	2.79	0.47(0.17)	2.68

Maternal age	-0.03(0.05)	-0.62	-0.02(0.05)	-0.47	-0.03(0.05)	-0.62	-0.02(0.05)	-0.47	-0.04(0.05)	-0.67	-0.04(0.05)	-0.84
Lamb age^2	0.02(0.10)	0.16	-	-	0.02(0.10)	0.16	-	-	-0.008(0.10)	-0.08	-	-
HR quality	-0.05(0.11)	-0.45	-	-	-0.05(0.11)	-0.45	-	-	-	-	-	-
HR quality^2	-0.12(0.09)	-1.29	-	-	-0.12(0.09)	-1.29	-	-	-	-	-	-
Lamb age:HR quality	0.07(0.06)	1.08	-	-	0.07(0.07)	1.08	-	-	-	-	-	-
PC1	-	-	-	-	-	-	-	-	-0.05(0.06)	-0.84	-	-
PC2	-	-	-	-	-	-	-	-	-0.12(0.11)	-1.09	-0.10(0.06)	-1.65
PC3	-	-	-	-	-	-	-	-	-0.04(0.14)	-0.31	-	-
Lamb age:PC1	-	-	-	-	-	-	-	-	-0.08(0.05)	-1.74	-	-
Lamb age:PC2	-	-	-	-	-	-	-	-	-0.16(0.08)	-1.99	-0.08(0.05)	-1.59
Lamb age:PC3	-	-	-	-	-	-	-	-	0.003(0.09)	0.03	-	-

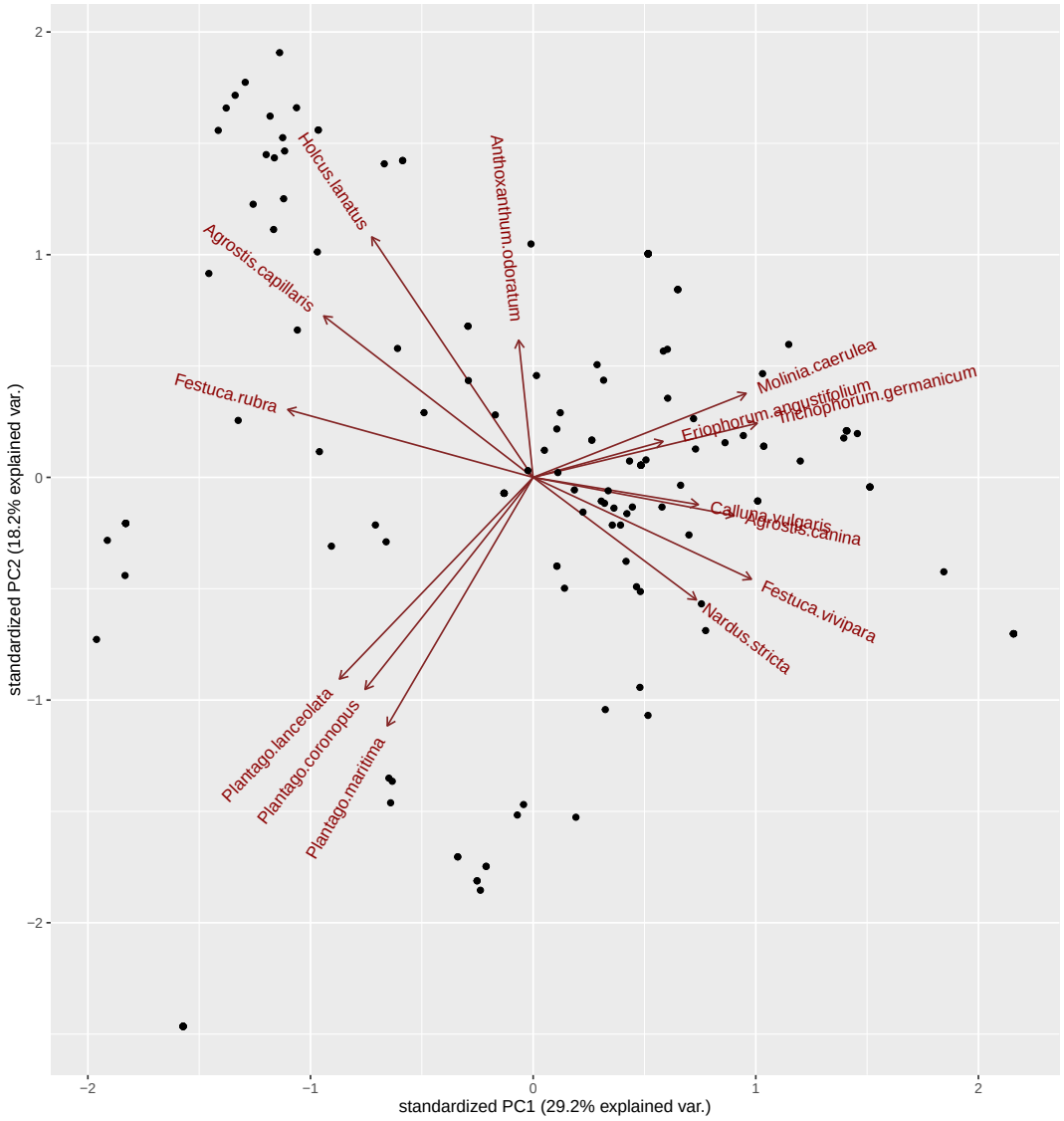

Figure S1: First and second principal components as used in individual resource selection functions. These were derived from a principal components analysis (PCA) of hectare percentage cover estimates for the 14 most common plant species on St. Kilda

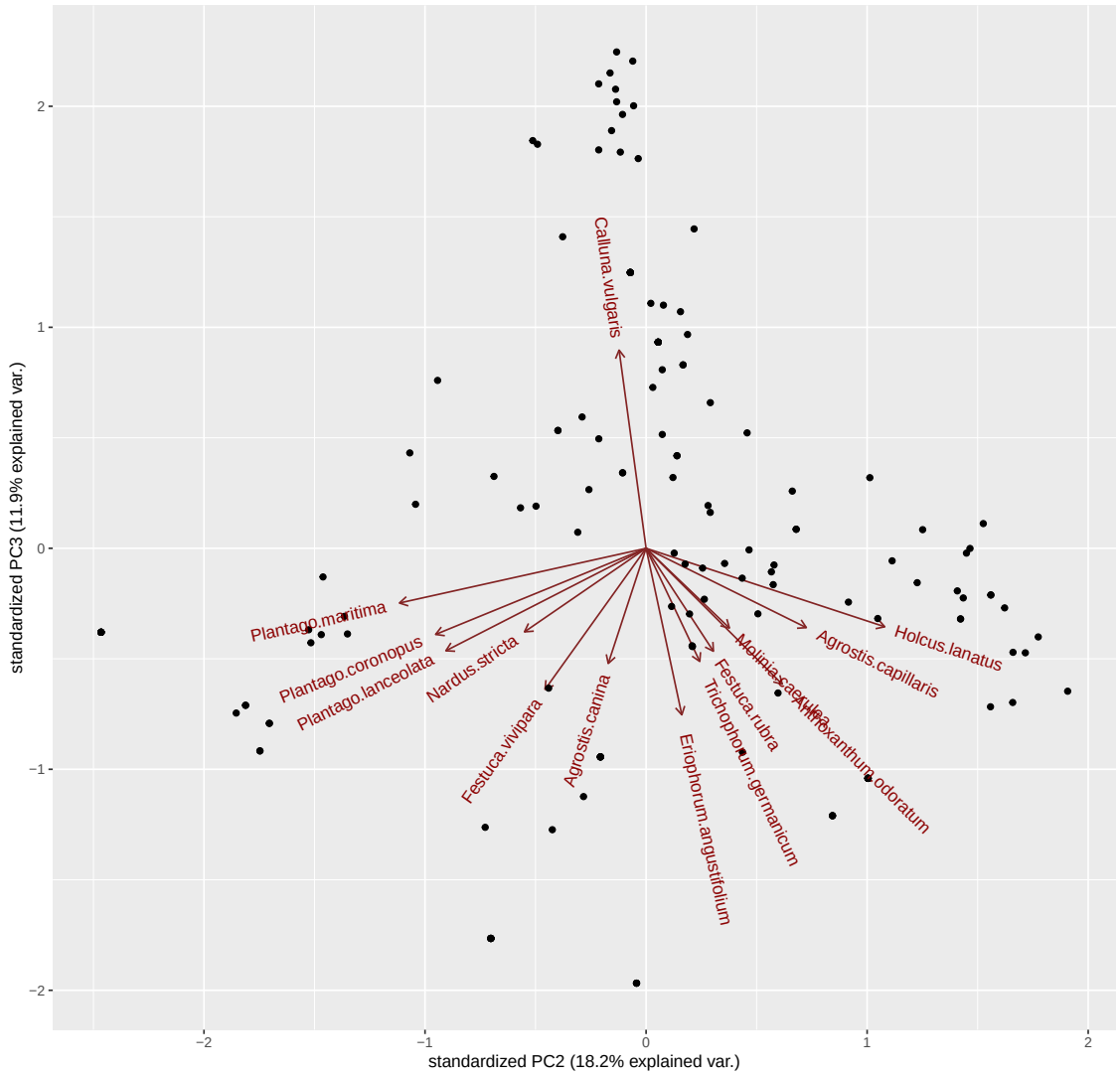

Figure S2: Second and third principal components as used in individual resource selection functions. These were derived from a principal components analysis (PCA) of hectare percentage cover estimates for the 14 most common plant species on St. Kilda

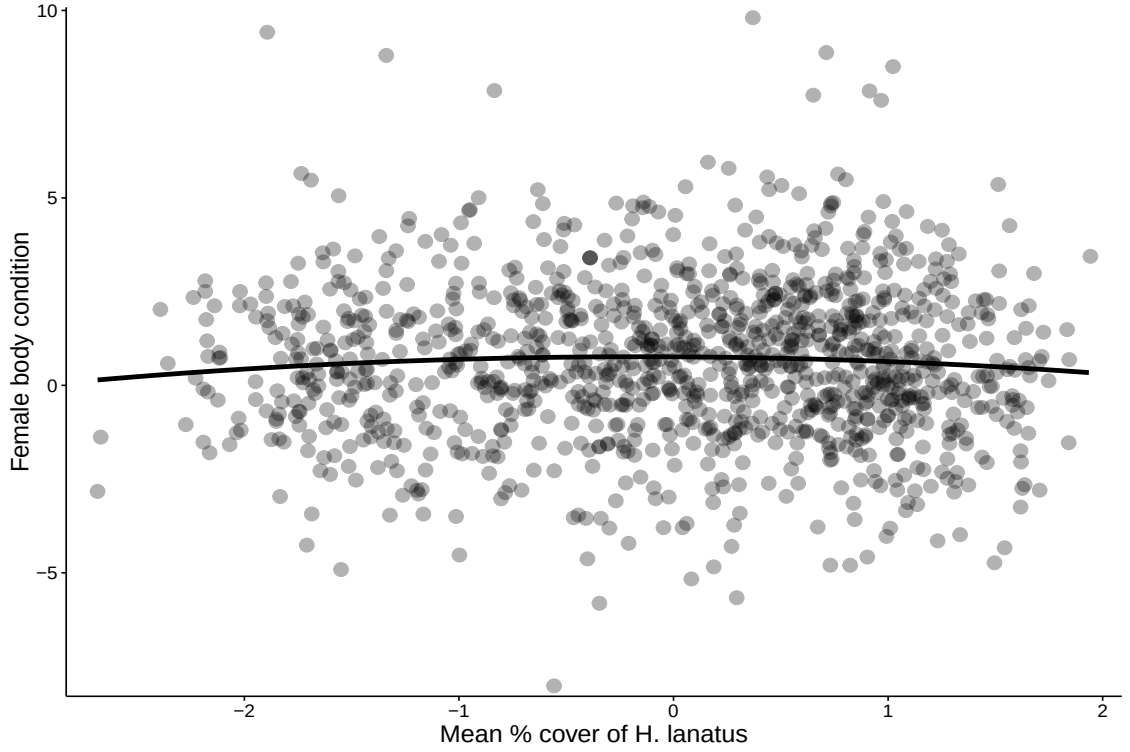

Figure S3: Female body condition (measured as the residuals of a linear regression of body mass against leg length) plotted against home range quality (the mean percentage cover of *H.lanatus* in a female's home range in the year preceding the birth of a lamb). The regression line comes from the full linear mixed model

Appendix B

Supplementary material for Chapter 4

Appendix S1: Example R code for the analysis of birth weight

```
library(Matrix)

library(MASS)

library(asreml)

library(nadiv)


X2.grm<-read.table(file="GRM for birth weight.txt",header=TRUE) #reading in the genomic relatedness matrix

colnames(X2.grm)<-row.names(X2.grm)

X2.grm<-as.matrix(X2.grm) #converting the GRM from dataframe to matrix


pheno<-read.table(file="Birth weight data for supplementary.txt",header=TRUE) #reading in the phenotypic data


#and ensuring all the variables are read properly

pheno$ANIMAL<-as.factor(pheno$ANIMAL)

pheno$MOTHER<-as.factor(pheno$MOTHER)

pheno$BWEIGHT<-as.numeric(pheno$BWEIGHT)

pheno$CAPAGE<-as.factor(as.numeric(pheno$CAPAGE))

pheno$BYEAR<-as.factor(pheno$BYEAR)

pheno$SEX<-as.factor(pheno$SEX)

pheno$TWIN<-as.factor(pheno$TWIN)

pheno$MATAGE<-as.numeric(pheno$MATAGE)

pheno$MATAGEQUAD<-pheno$MATAGE^2

colnames(pheno)[9]<-"col"

colnames(pheno)[10]<-"row"

pheno$col<-as.factor(pheno$col)

pheno$row<-as.factor(pheno$row)
```

```
space<-read.table("Birth weight S matrix for supplementary.txt",header=TRUE) #reading in the S matrix

colnames(space)<-rownames(space)

space<-as.matrix(space)

space<-as(solve(space),"dgCMatrix") #getting the inverse of the above matrix for use in models


#first running a model with no random effects

model0<-asreml(fixed=BWEIGHT~1+CAPAGE+SEX+MATAGE+TWIN+MATAGEQUAD,data=pheno)


#then including a random effect to estimate the additive genetic variance

model1<-asreml(fixed=BWEIGHT~1+CAPAGE+SEX+MATAGE+TWIN+MATAGEQUAD,

        random=~giv(ANIMAL),data=pheno,ginverse=list(ANIMAL=X2.grm))


#calculate the chi-squared stat for the log-likelihood ratio test

2*(model1$loglik-model0$loglik)


#calculate the associated significance

1-pchisq(2*(model1$loglik-model0$loglik),1)


#now to calculate the heritability with its standard error

nadiv:::pin(model1,h2~V1/(V1+V2))


#then adding a term to partition the variance due to differences in the year of birth

model2<-asreml(fixed=BWEIGHT~1+CAPAGE+SEX+MATAGE+TWIN+MATAGEQUAD,

        random=~giv(ANIMAL)+BYEAR,data=pheno,ginverse=list(ANIMAL=X2.grm))


#determining whether the addition of this term improved model fit
```

```
2*(model2$loglik-model1$loglik)

1-pchisq(2*(model2$loglik-model1$loglik),1)


#then calculating the proportion of the total variance (conditioning on fixed effects) explained by each of the random effects

nadiv:::pin(model2,h2~V1/(V1+V2+V3))

nadiv:::pin(model2,byear~V2/(V1+V2+V3))


#now partitioning the variance attributable to maternal effects (both genetic and environmental)

model3<-asreml(fixed=BWEIGHT~1+CAPAGE+SEX+MATAGE+TWIN+MATAGEQUAD,


random=~giv(ANIMAL)+BYEAR+ide(MOTHER),data=pheno,ginverse=list(ANIMAL=X2.grm,MOTHER=X2.grm))


#again testing the significance of this term

2*(model3$loglik-model2$loglik)

1-pchisq(2*(model3$loglik-model2$loglik),1)


#now calculating the proportion of variance attributable to each term

nadiv:::pin(model3,h2~V1/(V1+V2+V3+V4))

nadiv:::pin(model3,byear~V2/(V1+V2+V3+V4))

nadiv:::pin(model3,m2~V3/(V1+V2+V3+V4))


#now separating the maternal effect into maternal genetic and maternal perm env

model4<-asreml(fixed=BWEIGHT~1+CAPAGE+SEX+MATAGE+TWIN+MATAGEQUAD,


random=~giv(ANIMAL)+BYEAR+ide(MOTHER)+giv(MOTHER),data=pheno,ginverse=list(ANIMAL=X2.grm,MOTHER=X2.grm),

        workspace=300e6,pworkspace=300e6 )
```

```
#testing significance

2*(model4$loglik-model3$loglik)

1-pchisq(2*(model4$loglik-model3$loglik),1)


#and calculating the proportion of variance accounted for by each random term

nadiv:::pin(model4,h2~V1/(V1+V2+V3+V4+V5))

nadiv:::pin(model4,byear~V2/(V1+V2+V3+V4+V5))

nadiv:::pin(model4,matenv~V3/(V1+V2+V3+V4+V5))

nadiv:::pin(model4,matgen~V4/(V1+V2+V3+V4+V5))


#adding in additive-maternal genetic covariance

model5<-asreml(fixed=BWEIGHT~1+CAPAGE+SEX+MATAGE+TWIN+MATAGEQUAD,

        random=~str(~giv(ANIMAL)+giv(MOTHER),
~us(2):giv(ANIMAL))+BYEAR+ide(MOTHER),data=pheno,ginverse=list(ANIMAL=X2.grm,MOTHER=X2.
grm),

        workspace=300e6,pworkspace=300e6)


2*(model5$loglik-model4$loglik)

1-pchisq(2*(model5$loglik-model4$loglik),1)


#calculating the proportions of variance accounted for by each random term

nadiv:::pin(model5,h2~V1/(V1+V3+V4+V5+V6))

nadiv:::pin(model5,matgen~V3/(V1+V3+V4+V5+V6))

nadiv:::pin(model5,byear~V4/(V1+V3+V4+V5+V6))

nadiv:::pin(model5,matenv~V5/(V1+V3+V4+V5+V6))


#calculating the direct additive-maternal genetic correlation
```

```
nadiv:::pin(model5,ram~V2/(sqrt(V1*V3)))

#calculating the total heritability

nadiv:::pin(model5,toth~(V1+1.5*V2+0.5*V3)/(V1+V2+V3+V4+V5+V6))


#incorporating the S matrix

#first you have to make another column of mother IDs in order to associate the matrix with it

pheno$MOTHER2<-pheno$MOTHER

space<-as.matrix(space)


model6<-asreml(fixed=BWEIGHT~1+CAPAGE+SEX+MATAGE+TWIN+MATAGEQUAD,

        random=~str(~giv(ANIMAL)+giv(MOTHER),
~us(2):giv(ANIMAL))+BYEAR+ide(MOTHER)+giv(MOTHER2),data=pheno,


ginverse=list(ANIMAL=X2.grm,MOTHER=X2.grm,MOTHER2=space),workspace=300e6,pworkspace=3
00e6)


2*(model6$loglik-model5$loglik)

1-pchisq(2*(model6$loglik-model5$loglik),1)


#calculating the proportions

nadiv:::pin(model6,h2~V1/(V1+V3+V4+V5+V6+V7))

nadiv:::pin(model6,matgen~V3/(V1+V3+V4+V5+V6+V7))

nadiv:::pin(model6,byear~V4/(V1+V3+V4+V5+V6+V7))

nadiv:::pin(model6,matenv~V5/(V1+V3+V4+V5+V6+V7))

nadiv:::pin(model6,space~V6/(V1+V3+V4+V5+V6+V7))


#additive-maternal genetic correlation

nadiv:::pin(model6,ram~V2/(sqrt(V1*V3)))

#total heritability
```

```
nadiv:::pin(model6,toth~(V1+1.5*V2+0.5*V3)/(V1+V2+V3+V4+V5+V6+V7))


#now using the autoregressive approach


model7<-asreml(fixed=BWEIGHT~1+CAPAGE+SEX+TWIN+MATAGE+MATAGEQUAD,

        random=~str(~giv(ANIMAL)+giv(MOTHER),
~us(2):giv(ANIMAL))+BYEAR+ide(MOTHER)+mtrnv(row,col,phi="0.1U",nu="0.5F",lambda="1.0F"),


data=pheno,ginverse=list(ANIMAL=X2.grm,MOTHER=X2.grm),workspace=300e6,pworkspace=300e6)


2*(model7$loglik-model5$loglik)

1-pchisq(2*(model7$loglik-model5$loglik),1)


#calculating proportions

nadiv:::pin(model7,h2~V1/(V1+V3+V4+V5+V11+V12))

nadiv:::pin(model7,matgen~V3/(V1+V3+V4+V5+V11+V12))

nadiv:::pin(model7,byear~V4/(V1+V3+V4+V5+V11+V12))

nadiv:::pin(model7,matenv~V5/(V1+V3+V4+V5+V11+V12))

nadiv:::pin(model7,space~V11/(V1+V3+V4+V5+V11+V12))


#additive-maternal genetic correlation

nadiv:::pin(model7,ram~V2/(sqrt(V1*V3)))

#total heritability

nadiv:::pin(model7,toth~(V1+1.5*V2+0.5*V3)/(V1+V2+V3+V4+V5+V11+V12))
```

Appendix C

Papers produced during this project

ECOLOGY LETTERS

Ecology Letters, (2015) doi: 10.1111/ele.12550

LETTER

Sex differences in relationships between habitat use and reproductive performance in Soay sheep (*Ovis aries*)

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Abstract

The role of habitat use in generating individual variation in fitness has rarely been examined empirically in natural populations of long-lived mammals, particularly for both sexes simultaneously. This is the case despite the increase in studies attempting to understand evolutionary change in such populations. Using data from the St. Kilda Soay sheep population, we quantified the association between lifetime reproductive performance (lifetime breeding and reproductive success) and the proportion of the home range covered by a key grass species, *H. lanatus,* for 490 females and 304 males. Increased *H. lanatus* cover was associated only with increased female lifetime reproductive success, but increased lifetime breeding success for both sexes, arising through increased male longevity and increased female fecundity. This work suggests that improved understanding of the causes and consequences of fitness differences will likely require us to better account for habitat-derived individual variation, and to do so for the sexes appropriately.

Keywords

Fitness, grassland, habitat use, heathland, home range, lifetime reproductive success (LRS), Scotland, Soay sheep, St Kilda.

Ecology Letters (2015)

INTRODUCTION

Understanding the causes of variation in the relative contribution of individuals to the next generation is key to research in any field of evolutionary ecology. Long-term longitudinal studies of marked birds and mammals, by enabling the breeding success of individuals to be tracked throughout their life, have made it possible to derive estimates of Darwinian fitness through the calculation of lifetime breeding (LBS) or lifetime reproductive success (LRS) (Grafen 1982; Brommer *et al.* 2004).

In species or sexes with parental care, LRS is traditionally thought to consist of four components; survival to reproductive age, reproductive longevity, offspring production and offspring survival (Clutton-brock 1988). Individual differences in any one or a combination of these components can generate individual variation in LRS. Indeed, there are numerous studies documenting the roles of longevity (Pettorelli & M. Durant 2007; Robbins *et al.* 2011), fecundity (Cassinello & Alados 1996; Von Holst *et al.* 2002) and offspring survival (Von Holst *et al.* 2002) in explaining between individual differences in LRS in a variety of species. Where parental care is absent, LBS is traditionally used as a measure of fitness, consisting of no component relating to offspring survival.

Both individual traits and environmental factors can impact LBS and LRS by influencing these components. LRS has been shown to vary with individual traits such as tawny owl (*Strix aluco*) colour morph (Brommer *et al.* 2005), and body size in male red deer (*Cervus elaphus*) (Kruuk *et al.* 1999). The environmental factors that can influence an individual's fitness are diverse. For example LRS can be affected by the number and organisation of conspecifics, for instance higher population density negatively impacts the number of fawns born to female red deer that survive to 2 years of age (Kruuk *et al.* 1999). Furthermore, differences in habitat use, acting via factors such as resource availability can result in fitness variation. In fact, many ecological ideas, including optimal foraging theory (MacArthur & Pianka 1966) and the concept of the ecological niche (Grinnell 1917; Hutchinson 1957), hinge on the existence of fitness–habitat relationships.

Assessments of the link between fitness and habitat use or selection require data based on observations of identifiable individuals over their entire life. Such data are rare, particularly for long-lived species such as large herbivores, and therefore such studies are scarce. Nevertheless, in female red deer on the Isle of Rum in Scotland, selection for *Agrostis*/*Festuca* grassland is positively associated with LRS (McLoughlin *et al.* 2006). Similarly, in the Trois Fontaines population of roe deer (*Capreolus capreolus*), the amount of meadowland in a female's home range was associated with more than a twofold increase in the number of fawns weaned (McLoughlin *et al.* 2007).

Bridging the gaps in our knowledge of habitat–reproductive success relationships could prove valuable in many ways. We have only recently begun to appreciate the extent to which estimates of quantitative genetic parameters in wild animals can be biased by not accounting for spatial sources of variation/similarity between individuals (Stopher *et al.* 2012). For example if related individuals also share similar habitat, we could inflate the estimate of heritability by ignoring the fact

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that some of the similarity in the value of a trait may not be due to shared genes (Stopher *et al*. 2012). Demonstrating the prevalence of spatial similarities in individual fitness will hopefully improve the appreciation of this potential non-genetic source of similarity, something that will be central to understanding evolutionary dynamics in nature. The wider understanding of the intricate relationships between lifetime reproductive performance and habitat characteristics also has the potential to be important in an applied setting, as the successful conservation and management of organisms must be based on scientific understanding of the impact of environmental factors on both survival and breeding success.

We aimed to use the extensive long-term data set for the St. Kilda Soay sheep (*Ovis aries*) to investigate habitat–performance relationships for both sexes. This work builds on the finding that the Soay sheep population can be divided into three hefts, spatial subdivisions that vary in survival, recruitment and dispersal rates probably due to variation in the quality of grazing (Coulson *et al*. 1999). We now have the ecological data to investigate relationships between grazing quality and demographic parameters for the St. Kilda Soay sheep population at a relatively fine home range scale. We therefore investigated whether home range variation, specifically in the cover of a grass species *Holcus lanatus*, was associated with variation in male and female reproductive performance (LBS and LRS), and if so which components of reproductive performance (longevity, fecundity and lamb survival) were most tightly linked to this habitat variation. We chose this grass species because it is a key component of *Holcus-Agrostis* grassland, the most productive island community (as determined using grazing exclosures), containing the highest live standing-crop biomass (Crawley *et al*. 2004). In addition, habitat selection indices have shown this grassland community to be highly palatable to the sheep (Crawley *et al*. 2004). Body weight is associated with survival and fecundity in both sexes (Clutton-Brock *et al*. 1996; Milner *et al*. 1999; Preston *et al*. 2003), with body weight likely linked to forage availability. We might therefore expect that individuals with home ranges containing high percentage covers of *H. lanatus* will have higher LBS/LRS. However, male reproductive success is heavily dependent on horn type (Robinson *et al*. 2006), horn size (Preston *et al*. 2003) and testes size (Preston *et al*. 2003) and there is no evidence in the Soay sheep that these traits are related to habitat use. As a result of this we hypothesised that only female reproductive performance would vary with *H. lanatus* cover.

METHODS

Study area and animals

The data in this study come from the Soay sheep population on the island of Hirta in the St. Kilda archipelago, Scotland (57°49′ N 08°34′ W). One hundred and seven sheep were introduced to Hirta from the neighbouring island of Soay in 1932, following the evacuation of the local human population (Clutton-brock *et al*. 2004). Since its introduction the population has been entirely unmanaged and Hirta is now home to between 600 and 2300 Soay sheep, depending on variation in mortality between years. The sheep on Hirta have been the subject of research since the early 1960s, and the Village Bay population intensively studied since 1985.

The Village Bay study area is 170 hectares in size, and contains *c*. 30% of the total island sheep population (Clutton-Brock *et al*. 1992). The study area contains two broad vegetation types: one being the grassland present on the previously cultivated ground (known as the 'inbye') and the other being the heather-rich (*Calluna vulgaris*) moorlands dominating the 'outbye' (Gwynne *et al*. 1974). At a finer scale, Village Bay can be divided into a number of major plant community types. The inbye is dominated by *Holcus-Agrostis* (HA) grassland, the most productive community type with the highest live standing-crop biomass (Crawley *et al*. 2004), whereas the major outbye communities include *Calluna* and *Nardus* dominated wet-heath and dryer *Calluna* heath (Jones *et al*. 2006).

Individual Soay sheep are marked with plastic ear tags shortly after birth to enable identification, and more than 95% of animals residing in Village Bay bear tags (Coltman *et al*. 1999b). Regular censuses and mortality searches enable the mortality status of animals to be tracked, whilst also providing information on individual space use. The data analysed in this paper come from sheep born in/after 1985, with known birth dates, that survived to at least one year of age, and had been confirmed dead by the end of 2013.

Home-range estimation

Researchers visit the island three times per year (April–May, July–August, October–November), and during each trip they conduct ten censuses of the entire study area, recording the locations of all individuals. We extracted lifetime census observations for each individual and transformed them onto a grid, with the most south-westerly census observation (NF091993) becoming (0,0). Each step on the grid therefore represented a distance of 100 m. Though the final trip takes place over the rut, where we see a break down in the social segregation observed throughout the rest of the year (Grubb & Jewell 1974), we used census observations from all trips to calculate core home ranges. This is because the area used by a male during the rut is likely to be important to their reproductive performance. Ideally we would calculate home ranges for periods of social segregation and aggregation separately, but calculating a rut home range would only be possible for a small number of males with the necessary number of observations. Using all available observations therefore may, to some extent, mask any relationship between LRS/LBS and habitat use specifically during sexual segregation or aggregation. We estimated home ranges using kernel density methods with the package 'adehabitatHR' (Calenge 2006) in R version 3.0.2 (R Development Core Team 2008), calculating the smoothing parameter using the *ad hoc* method. During censuses animals are assigned a grid reference to the nearest 100 m, and therefore many observations have identical grid references which can cause problems when estimating home ranges using kernel methods (Tufto *et al*. 1996). To overcome this, a random number between −20 and 20 (representing a distance of up to 20 metres) was added to the X and Y coordinates for each census record. Using established methods (see Section 1 in the

supporting information, and Powell 2000) we calculated that the core home range for both sexes was that with a 70% isopleth.

We carried out incremental area analysis to determine the number of observations needed to give an asymptote in core home-range area. To accurately estimate home ranges we needed at least 49 observations for females, and 39 for males (see section 2 in the Supporting Information), leaving us with 490 females and 304 males on which to conduct the analyses. Of these, 276 females and 69 males had observations in every year of life, whereas 209 females and 229 males were missing observations in 1 year. Of these, 205 females and 229 males lacked observations in their death year, and the remaining four females lacked observations in their birth year. Only five females and six males lacked observations in more than 1 year. Females tended to have a greater number of observations than males [females = 140 ± 90, males = 67 ± 50 (mean ± SD)], probably because average male longevity in our sample (4 years) was half that of females and consequently males tended to have been seen in fewer censuses. To evaluate whether our results were robust to the number of observations available for home range estimation we repeated the analyses for individuals with ≥ 100 census observations (364 females, 100 males).

Based on the Ordnance Survey Grid, the study area has been divided into 160 one hectare squares (100 × 100 m) [the remaining 10 hectares were not surveyed for vegetation due to access difficulties and/or a lack of vegetation (some are covered by scree)]. Between 2008 and 2012 complete species lists were compiled for the vascular plants in each hectare, and the percentage cover of each species was scored by eye (to the nearest 5%). All botanical data were collected by MJC so there were no between-observer sources of error. Ocular cover estimates have been calibrated against sorted biomass samples in related studies. For example visual cover estimates (Williams 1978) and biomass samples (Crawley *et al*. 2005) were compared for 87 plots on the Park Grass Experiment at Rothamsted, with the correlation between the two methods exceeding $r = 0.87$ for all species present on more than 20 plots (MJC, unpublished analysis) (see also Allan & Crawley 2011). Furthermore, visual cover estimation is the only practical method for hectare-sized plots because it averages over the within-plot spatial heterogeneity. The boundaries of the plant communities used in this study are in the same locations as described in Gwynne *et al*. (1974), with no detectable change in botanical composition within the communities since detailed botanical recording began in 1993 (MJC, unpublished results). We calculated the percentage cover of *H. lanatus* in individual core home ranges by taking a weighted mean of the percentage cover across the grid squares contained within the home range. We used the proportion of the grid square contained within the home range as a weight thereby taking into account the varying contributions of grid squares when determining home range quality.

Lifetime reproductive and lifetime breeding success

We calculated LBS as the number of lambs born over an individual's lifetime, and LRS as the number of these lambs that survived to their first August census, denoting survival to weaning and recruitment into the population (Clutton-brock *et al*. 2004). Lambs with unknown death dates that were not seen in the August following birth or in subsequent years, were excluded to ensure conservative reproductive performance estimates as we could not be sure they survived to recruitment. We deduced mother–offspring relatedness from field observations and in some cases by genetic methods (see below). Paternity is impossible to determine from field observations because females mate with multiple males whilst in oestrus (Coltman *et al*. 1999a,b), therefore father–offspring relatedness was determined exclusively using molecular parentage analysis. Paternities for 50% (814) of lambs were inferred with 100% confidence using 315 high minor allele frequency, unlinked single nucleotide polymorphisms (SNPs) in the R package 'MasterBayes' (Hadfield *et al*. 2006; for details see Bérénos *et al*. 2014). For those cases where parentage inferences could not be made using SNP genotypes alone (not all offspring and candidate parents were successfully genotyped, particularly individuals alive prior to 1990), paternities derived using microsatellites were used if the confidence of the assignment was ≥ 95% (Morrissey *et al*. 2012) (807 lambs). See Fig. 1 for the distributions of male and female LRS.

To explore which components of individual reproductive performance were most tightly linked with spatial variation in habitat quality we considered additional response variables. These were (1) fecundity: the number of lambs born to an individual divided by longevity and (2) longevity: the age, in years, at the time of death. For females, we also considered offspring survival: the proportion of lambs that survived to their first August census.

Data analysis

LRS/LBS and their components were analysed using linear and generalised linear models (GLMs) in R version 3.0.2 (R Development Core Team, 2008). The sexes were analysed separately due to the marked difference in the distributions of *H. lanatus* covers [females = 35 ± 13, males = 10 ± 5 (mean ± SD)]. We assessed the effect of the following factors: (1) population density in the August of the individual's year of birth (number of yearlings and adults present in Village Bay) because population density in early life causes long-term cohort variation in traits of both male and female Soay sheep (Coltman *et al*. 1999a,b; Forchhammer *et al*. 2001) and (2) the mean percentage cover of *Holcus lanatus* to test for an effect of home range quality on reproductive performance. We also included a quadratic term for the mean percentage cover of *Holcus lanatus* to determine if a nonlinear relationship was a better fit to the data. Both explanatory variables were mean centred prior to analysis to simplify the interpretation of the results and to reduce collinearity between power terms.

We assumed a Poisson distribution for LRS, LBS and longevity, a Gaussian distribution for fecundity, and a binomial distribution for lamb survival. We corrected for over-dispersion in the case of LRS, LBS, longevity and lamb survival by using quasi-GLM models (Crawley 2007). Model selection was performed using Akaike's Information Criterion corrected for small sample size (AICc), with the best model taken to be

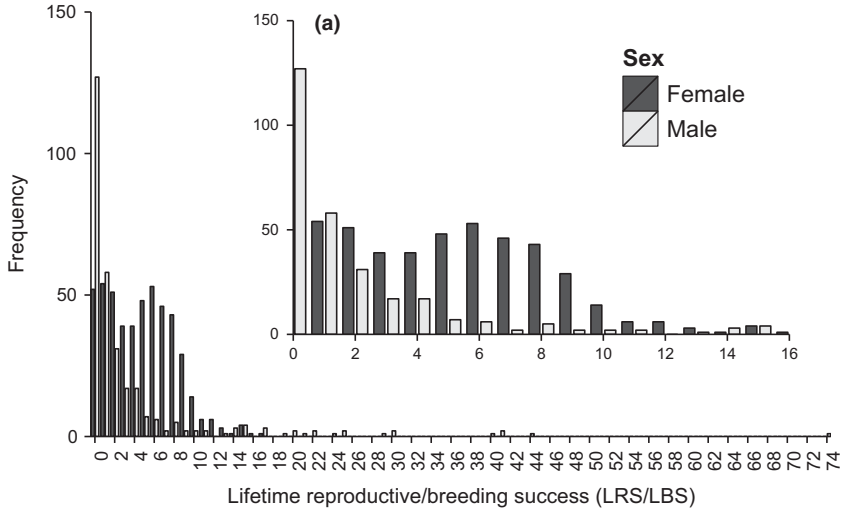

Figure 1 Distributions of LRS for the 490 female (mean 4.77 ± 3.41 SD) and 304 male (3.67 ± 8.09) Soay sheep from the island of Hirta, Scotland, on which the analyses reported in this study were conducted. Maximum LRS was 17 for females and 74 for males. The inset figure (a) shows a zoomed in view of the distributions up to LRS of 16.

that with the lowest AICc value (Burnham & Anderson 2002). QAICc was used for quasi-GLM models, and models containing all possible explanatory variable combinations were compared.

Models where ΔAIC < 2 are not considered to be meaningfully different (Burnham & Anderson 2002), however, where these models differ by one parameter, the larger model may not actually be competitive, being within two AIC units only because it contains one additional parameter (Arnold 2010). To counteract this '2 ΔAIC problem' we used two methods recommended by Arnold (2010). First, we have reported all models and used log-likelihood comparisons to determine whether the addition of a single parameter was informative. Second, we used parameter estimates from model averaging to assess the importance of the addition of explanatory variables. We employed model averaging when model selection resulted in models with an AICc/QAICc difference of < 2 units compared to the model with the lowest AICc/QAICc. We used the R package *'MuMIn'* (Barton 2015) to take parameter estimates from the best model and competing models, weight them by AIC weights (ω) and sum them to give predictions of the average model. Where a model averaging approach was used we report estimates from both the best model and the averaged model in the results tables.

RESULTS

LRS, LBS and their components

Female LBS and LRS were strongly positively correlated with female longevity and fecundity (Table 1). Both measures were also positively correlated with offspring survival; however, the correlation was stronger for LRS (Table 1). Male LBS and LRS were also positively correlated with longevity and fecundity, though these correlations were slightly weaker than in the case of females (Table 1).

Female reproductive success

We found evidence for habitat-related variation in female reproductive performance, with the percentage cover of *H. lanatus* featuring in the best model for LBS and LRS (Table S1). LBS increased by 31%, and LRS by 34% as *H. lanatus* cover increased from 5 to 58%, equating to more than one lamb in both cases (Table 2; Fig. 2). Log-likelihood comparisons of competing models and model averaging suggested that the relationship between LRS/LBS and the percentage cover of *H. lanatus* was best described by the linear term (Table 2). Density also explained variation in LRS and LBS (Table S1), with an increase from 132 to 475 individuals associated with a 25% decrease in LBS and 29% decrease in LRS (Table 2).

When we considered individuals with ≥ 100 observations, the models with the most support again indicated that LBS and LRS were related to *H. lanatus* availability (Table S2 and

Table 1 Correlation coefficients between LRS/LBS and their components for females and males

Reproductive performance metric	Component	Correlation coefficient
Female		
LBS	Longevity	0.78***[a]
LBS	Fecundity	0.80***
LBS	Offspring survival	0.27***
LRS	Longevity	0.75***
LRS	Fecundity	0.71***
LRS	Offspring survival	0.51***
Male		
LBS	Longevity	0.60***
LBS	Fecundity	0.54***
LRS	Longevity	0.59***
LRS	Fecundity	0.53***

[a]Asterisks indicate significance level: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

S3). However, in contrast to the analysis of individuals with ≥ 49 observations, support for the model containing the quadratic term indicated that these relationships were nonlinear (Table S3), and that at the highest *H. lanatus* covers there was a reduction in LBS and LRS (Fig. S1). The results for density were consistent, with LBS decreasing by 27% and LRS by 32% as density increased from 132 to 450 individuals (Table S3).

We also found evidence for a positive linear relationship between fecundity and the percentage cover of *H. lanatus,* with the linear *H. lanatus* term retained in the best model (Table S1), and no indication that adding the quadratic term improved model fit (Table 2 and S1). Fecundity increased by 12% as *H. lanatus* cover increased from 5 to 58% (Table 2, Fig. S2), and this increase was still evident when considering individuals with ≥ 100 observations (Table S3, Fig. S3).

The models with the most support indicated that neither longevity nor offspring survival were related to *H. lanatus* availability (Table S1). Models including the mean percentage cover of *H. lanatus* were identified as competitive; however, log-likelihood comparisons (Table S1) indicated that the incorporation of *H. lanatus* cover was not informative. Again, these results were consistent when we considered individuals with ≥ 100 observations (Table S2 and S3).

Table 2 Parameter values for the best models (and model averaging) describing the relationships between female reproductive performance and the mean proportion of *H. lanatus* grassland in the core home range. This analysis includes those individuals with at least 49 observations for delimiting their home range

Term	Parameter estimate (SE)	t/z*	P
Female LBS best model			
Percentage *H. lanatus*	5.1×10^3 (2.1×10^3)	2.41	0.016
Density	8.4×10^{-4} (3.6×10^{-4})	−2.32	0.021
Model averaged			
Percentage *H. lanatus*	5.1×10^3 (2.1×10^3)	2.38	0.017
Density	-8.3×10^{-4} (4.2×10^{-4})	2.30	0.021
Percentage *H. lanatus*^{2}	-1.6×10^{-5} (9.6×10^{-5})	0.16	0.868
Female LRS best model			
Percentage *H. lanatus*	5.5×10^3 (2.4×10^3)	2.25	0.025
Density	−0.001 (4.2×10^{-4})	−2.38	0.018
Model averaged			
Percentage *H. lanatus*	5.4×10^3 (2.5×10^3)	2.19	0.029
Density	-9.9×10^{-4} (4.2×10^{-4})	2.35	0.019
Percentage *H. lanatus*^{2}	-4.3×10^{-5} (1.3×10^{-4})	0.33	0.742
Fecundity best model			
Percentage *H. lanatus*	2.5×10^3 (1.1×10^3)	2.29	0.022
Density	-5.9×10^{-4} (1.9×10^{-4})	−3.17	0.002
Model averaged			
Percentage *H. lanatus*	2.5×10^3 (1.1×10^3)	2.29	0.022
Density	-5.9×10^{-4} (1.9×10^{-4})	3.17	0.002
Percentage *H. lanatus*^{2}	7.0×10^{-6} (4.8×10^{-5})	0.14	0.885
Longevity best model			
Density	-4.6×10^{-4} (2.5×10^{-4})	−1.82	0.070
Model averaged			
Percentage *H. lanatus*	7.8×10^{-4} (1.3×10^3)	0.594	0.552
Density	-3.1×10^{-4} (3.0×10^{-4})	1.03	0.305
Offspring survival best model			
Intercept	1.24 (0.05)	24.61	< 0.001
Model averaged			
Percentage *H. lanatus*	3.1×10^{-4} (1.8×10^3)	0.17	0.866
Density	-2.4×10^{-4} (5.2×10^{-4})	0.46	0.649

*z values were obtained from the model averaging procedure.

Males

We found evidence for habitat-related variation in male LBS but not in male LRS, with the mean percentage cover of *H. lanatus* featured only in the best fit model for LBS (Table 3 and S4). This model predicted an increase in LBS of 4.9 lambs as *H. lanatus* cover increased from 0 to 22% (Table S4, Fig. 2); however, the standard errors for this estimate were large. A competing model for LBS contained only density as an explanatory variable, but log-likelihood comparisons suggested that the inclusion of *H. lanatus* cover did improve model fit (Table S4). The percentage cover of *H. lanatus* featured in a competing model for male LRS, though the parameter estimate (and associated standard error) from the model averaging suggest it was not informative (Table 3 and S4). The best model for male longevity predicted a 60% increase as *H. lanatus* cover increased from 0 to 22%, equating to an increase in longevity of almost 2 years (Table 3 and S4, Fig. S4). As for females, density in the year of birth explained variation in a number of male traits, with an increase in density from 132 to 475 individuals associated with a 69% decline in LBS and 80% decline in LRS (Table 3). Longevity was the only trait where including density did not improve model fit (Table 3 and S4).

The results were largely consistent when we considered only individuals with ≥ 100 observations, with *H. lanatus* cover explaining variation in longevity, but not in LRS or fecundity (Tables S5 and S6, Fig. S5). One difference was apparent, with the best fit model for LBS no longer including the *H. lanatus* term (Table S5). The results regarding density were consistent, with all male measures, except longevity, declining with density (Table S6).

DISCUSSION

The long-term data available for the St. Kilda Soay sheep provide a valuable opportunity to develop our understanding of individual fitness–habitat relationships. As hypothesised, we only found evidence for habitat-related variation in female LRS. However, contrary to expectation, we found evidence for variation in LBS with habitat use in both sexes, but that this was mediated in different ways for the sexes, with longevity increased for males but fecundity increased for females. Due to the difficulty in following individuals in natural populations from birth to death it remains difficult to study habitat–performance relationships in the wild, with only a handful of examples from species such as red deer (McLoughlin *et al.* 2006) and roe deer (McLoughlin *et al.* 2007). Our results not only offer evidence for statistically significant habitat–performance relationships in another natural population, but to our knowledge, provide the first evidence for sex differences in these relationships. We therefore feel that our results illustrate the importance of accounting for habitat–performance relationships, and of doing so effectively for both sexes.

For Soay sheep females, a 53% increase in *H. lanatus* cover equated to a difference of more than one lamb in both LBS

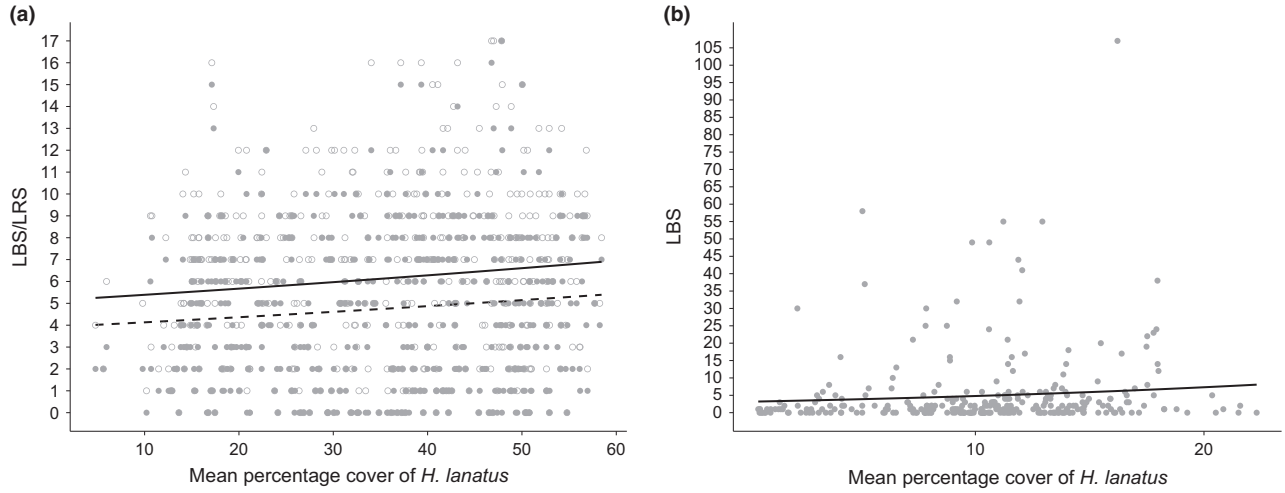

Figure 2 Lifetime breeding (LBS) (filled circles) and LRS (open circles) plotted against the mean percentage cover of *H. lanatus* in an individual's home range, (a) shows the data for females with at least 49 observations, whereas (b) shows the data for males with at least 39 observations (LRS is not plotted for males as we found no evidence for significant habitat-related variation). The regression lines come from the best fit generalised linear models (the solid lines represent the relationships for LBS whilst the dashed line represents the relationship for LRS).

Table 3 Parameter values for the best models (and model averaging) describing the relationships between male reproductive performance and the mean proportion of *H. lanatus* grassland in the core home range. This analysis includes those individuals with at least 39 observations for delimiting their home range

Term	Parameter estimate (SE)	t/z*	P
Male LBS best model			
Percentage *H. lanatus*	0.04 (0.03)	1.57	0.117
Density	-3.3×10^3 (1.6×10^3)	−2.10	0.036
Model averaged			
Percentage *H. lanatus*	0.03 (0.03)	0.91	0.362
Density	-3.5×10^3 (1.6×10^3)	2.13	0.033
Percentage *H. lanatus*^{2}	-4.8×10^{-4} (2.2×10^3)	0.21	0.832
Male LRS best model			
Density	-4.8×10^3 (1.6×10^3)	−2.89	0.004
Model averaged			
Percentage *H. lanatus*	0.02 (0.03)	0.62	0.538
Density	-4.6×10^3 (1.6×10^3)	2.78	0.005
Fecundity best model			
Density	-3.2×10^3 (1.0×10^3)	−3.10	0.002
Model averaged			
Percentage *H. lanatus*	0.01 (0.02)	0.68	0.499
Density	-3.1×10^3 (1.1×10^3)	2.92	0.003
Longevity best model			
Percentage *H. lanatus*	0.02 (6.0×10^3)	3.57	< 0.001
Model averaged			
Percentage *H. lanatus*	0.02 (6.1×10^3)	3.38	< 0.001
Density	-1.7×10^{-4} (3.1×10^{-4})	0.54	0.590
Percentage *H. lanatus*^{2}	-4.3×10^{-4} (1.0×10^{-4})	0.51	0.607

*z values were obtained from the model averaging procedure.

and LRS, driven by increased fecundity. The magnitude of this increase becomes apparent when we consider that this was a 31% increase in LBS and a 34% increase in LRS. Our results differed slightly when we considered only females with ≥ 100 census observations, with evidence for a small decline in LBS and LRS at the highest *H. lanatus* covers. This could result from density-dependent habitat selection, something known to occur in red deer (McLoughlin *et al.* 2006). This difference could, however, derive from conditioning on observation number and changing the distribution of *H. lanatus* covers. We census 30 times per year and therefore individuals can only be seen a maximum of 30 times each year. Therefore, by selecting individuals with ≥ 49 or ≥ 100 observations we also selected for individuals that survived to at least two or 4 years old respectively. By removing short-lived individuals, that may not be a random sample of the population with respect to their habitat use, we may have biased the parameter estimates. Our longevity results, however, suggest this was not the case, and indeed we see no evidence that the range of *H. lanatus* covers differed considerably for individuals with lifespans of up to 2 years [31 ± 12 (mean ± SD)] compared to all females [34 ± 13 (mean ± SD)].

The finding that female LRS varied with habitat use aligns well with what we know about their biology. Body weight is a key determinant of female fecundity (Clutton-Brock *et al.* 1996), and females also influence the growth of their lambs by providing milk (Clutton-Brock *et al.* 1992). Lactation is the most energetically demanding part of female mammalian reproduction (Clutton-Brock *et al.* 1989), and female mammals can and do modify their foraging behaviour to subsidise the costs of milk production (Barclay 1989). Perhaps, female Soay sheep with *H. lanatus* rich home ranges are better able to counteract the costs associated with lactation, enabling them to maintain their body condition and increase their fecundity.

Lamb survival did not change with *H. lanatus* cover, a pattern that seems counterintuitive given the strong LRS-offspring survival correlation and the importance of pre-weaning survival to the reproductive success of other ungulates such as roe deer (McLoughlin *et al.* 2007). One potential explanation is that Soay sheep are capital breeders, relying on body reserves to meet the energetic needs of reproduction (Stephens

et al. 2009). Because of this, pre-weaning survival of capital breeders tends to be less variable than income breeders (Gaillard *et al*. 1997). It is, however, possible that the explanation derives from some other aspect of their reproduction. For example, twinning rate is highly variable, ranging from 2 to 23% in adults (Clutton-brock *et al*. 2004) with heavier females having more twin litters (Clutton-brock *et al*. 2004). Twins are born lighter than singletons and experience lower survival (Clutton-Brock *et al*. 1992). Female body condition is likely higher in *H. lanatus* rich areas, and twin litters may be more common. Indeed, female mammals have been shown to adjust their litter size in relation to their condition (Risch *et al*. 2007; Servanty *et al*. 2007). The reduced survival of twins may contribute to the lack of any trend in offspring survival with *H. lanatus* cover.

In the case of males, the increase in longevity as *H. lanatus* cover increased seemed to translate into increased LBS, likely because they had a greater number of ruts in which to compete for matings. We must, however, remember that the standard errors around the parameter estimate for the *H. lanatus* effect were large. This may be because of the smaller sample size for males, and additional data may be needed to better establish the size of this effect. This increase in LBS with *H. lanatus* cover was not apparent when considering males with ≥ 100 observations, something that may be due to a further decrease in sample size or, as mentioned above, because of an inadvertent selection for males of longer lifespans, and a subsequent bias in the distribution of *H. lanatus* covers. The increase in longevity did not translate into increased LRS, and this may be because LRS was defined as the number of an individual's offspring that survived to recruitment. Given that only females provision lambs, males have little influence on the weaning success of their lambs besides the genes they contribute. Improved male body condition is therefore unlikely to translate into increased offspring survival, potentially explaining the lack of a relationship between male LRS and habitat use.

Though the result for LRS is intuitive given the biology of this species, our results may still have implications for the evolutionary study of this and other populations. The sex difference in the components of reproductive performance that varied with *H. lanatus* cover may prompt us to look for spatial variation in the selection on, and evolutionary potential of longevity and fecundity, and to understand whether this differs between the sexes. Our results may also have implications for sexual selection and the evolution of mating tactics. For example we may expect to see spatial variation in offspring sex ratios, as female philopatry could mean that females in *Holcus* rich areas can enhance their fitness by bearing daughters that will also have *Holcus* rich home ranges (Clutton-brock *et al*. 2004). Furthermore, males may be able to enhance their fitness by mating with females in *Holcus* rich areas due to their increased LRS. We may be better able to understand this in the future by looking exclusively at the relationship between rut home range characteristics and male LRS.

The results for density were generally consistent for the sexes, with the only difference being that high density in the year of birth seemed to have a larger detrimental effect on the reproductive success of males, likely due to the increase in competition for matings under these conditions. The population density of Soay sheep on St. Kilda is highly variable due to large fluctuations in winter mortality (Clutton-brock *et al*. 2004), and lambs born in high-density years are lighter both as yearlings and adults (Clutton-Brock *et al*. 1992; Forchhammer *et al*. 2001). We found that individuals born in high-density years had lower LBS and LRS, and this aligns with previous work showing marked cohort variation in both mortality and fecundity in this population (Coltman *et al*. 1999a,b; Clutton-brock *et al*. 2004). We considered density in the year of birth due to its known importance in this population, but foraging behaviour may also vary with density at other periods of an individual's life. Changes in density could therefore modify the relationship between habitat use and fitness, something that has been shown for female red deer (McLoughlin *et al*. 2006). The density dependence of the relationships we have found, along with an investigation into how foraging behaviour itself changes, would be an interesting avenue of research in the Soay sheep.

To our knowledge this is the only study to have simultaneously examined habitat–performance relationships for both sexes of a wild-living mammal. Where there is environmental heterogeneity in fitness related traits we may anticipate differences in population dynamics, genetics and in the speed/direction of evolutionary change. Indeed, we see spatial variation in Soay sheep population dynamics (Coulson *et al*. 1999), and in Sable island horses environmental heterogeneity is associated with variation in population dynamics and inbreeding prevalence (Contasti *et al*. 2012). To understand how populations will change in the future, predict whether we will see successful adaptation to changing conditions, or uncover why variation remains in some fitness related traits, accounting for environmental heterogeneity is essential. Knowing how variation in the environment differentially affects the sexes is an important step in this process.

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AUTHORSHIP

CR and MC conceptualised the work, CR performed the analysis and wrote the manuscript, MC and JGP collected the data, and MC and JMP aided in the interpretation of the data and helped to evaluate and edit the manuscript.

REFERENCES

Allan, E. & Crawley, M.J. (2011). Contrasting effects of insect and molluscan herbivores on plant diversity in a long-term field experiment. *Ecol. Lett.*, 14, 1246–1253.

Arnold, T.W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *J. Wildl. Manage.*, 74, 1175–1178.

Barclay, R.M.R. (1989). The effect of reproductive condition on the foraging behavior of female hoary bats, Lasiurus cinereus. *Behav. Ecol. Sociobiol.*, 24, 31–37.

Barton, K. (2015). MuMIn: Multi-model interference. R package version 1.14.0. Available at: http://CRAN.R-project.org/package = MuMIn. Last accessed 03/09/2015.

Bérénos, C., Ellis, P.A., Pilkington, J.G. & Pemberton, J.M. (2014). Estimating quantitative genetic parameters in wild populations: a comparison of pedigree and genomic approaches. *Mol. Ecol.*, 23, 3434–3451.

Brommer, J.E., Gustafsson, L., Pietiäinen, H. & Merilä, J. (2004). Single-generation estimates of individual fitness as proxies for long-term genetic contribution. *Am. Nat.*, 163, 505–517.

Brommer, J.E., Ahola, K. & Karstinen, T. (2005). The colour of fitness: plumage coloration and lifetime reproductive success in the tawny owl. *Proc. Biol. Sci.*, 272, 935–940.

Burnham, K.P. & Anderson, D.R. (2002). Information and likelihood theory: a basis for model selection. In: *Model Selection and Multimodel Inference*. Springer-Verlag New York, New York, pp. 49–97.

Calenge, C. (2006). The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Modell.*, 197, 516–519.

Cassinello, J. & Alados, C.L. (1996). Female reproductive success in captive Ammotragus lervia (Bovidae, Artiodactyla). Study of its components and effects of hierarchy and inbreeding. *J. Zool.*, 239, 141–153.

Clutton-brock, T.H. (1988). Reproductive success: studies of individual variation in contrasting breeding systems. In: *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (ed Clutton-Brock, T. H.). University of Chicago Press, Chicago, pp. 3–11.

Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1989). Fitness costs of gestation and lactation in wild mammals. *Nature*, 337, 260–262.

Clutton-Brock, T.H., Price, O.F., Albon, S.D. & Jewell, P.A. (1992). Early development and population fluctuations in Soay sheep. *J. Anim. Ecol.*, 61, 381–396.

Clutton-Brock, T.H., Stevenson, I.R., Marrow, P., MacColl, A.D., Houston, A.I. & McNamara, J.M. (1996). Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. *J. Anim. Ecol.*, 65, 675–689.

Clutton-brock, T.H., Pemberton, J.M., Coulson, T., Stevenson, I.R. & Maccoll, A.D.C. (2004). Individuals and populations. In: *Soay Sheep: Dynamics and Selection in an Island Population* (eds Clutton-Brock, T. H. & Pemberton, J. M.). Cambridge University Press, Cambridge, pp. 1–13.

Coltman, D.W., Bancroft, D.R., Robertson, A., Smith, J.A., Clutton-brock, T.H. & Pemberton, J.M. (1999a). Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. *Mol. Ecol.*, 8, 1199–1209.

Coltman, D.W., Smith, J.A., Bancroft, D.R., Pilkington, J., MacColl, A.D., Clutton-Brock, T.H. *et al.* (1999b). Density-dependent variation in lifetime breeding success and natural and sexual selection in Soay rams. *Am. Nat.*, 154, 730–746.

Contasti, A.L., Tissier, E.J., Johnstone, J.F. & McLoughlin, P.D. (2012). Explaining spatial heterogeneity in population dynamics and genetics from spatial variation in resources for a large herbivore. *PLoS ONE*, 7, 1–8.

Coulson, T., Albon, S., Pilkington, J. & Clutton-Brock, T. (1999). Small-scale spatial dynamics in a fluctuating ungulate population. *J. Anim. Ecol.*, 68, 658–671.

Crawley, M.J. (2007). Generalised linear models. In: *The R book*. John Wiley & Sons, Chichester, pp. 513–527.

Crawley, M.J., Albon, S.D., Bazely, D.R., Milner, J.M., Pilkington, J.G. & Tuke, A.L. (2004). Vegetation and sheep population dynamics In. *Soay Sheep: Dynamics and Selection in an Island Population* (eds Clutton-Brock, T. H. & Pemberton, J. M.) Cambridge University Press, Cambridge, pp. 89–111.

Crawley, M.J., Johnston, A.E., Silvertown, J., Dodd, M., de Mazancourt, C., Heard, M.S. *et al.* (2005). Determinants of species richness in the Park Grass Experiment. *Am. Nat.*, 165, 179–192.

Forchhammer, M.C., Clutton-Brock, T.H., Lindström, J. & Albon, S.D. (2001). Climate and population density induce long-term cohort variation in a northern ungulate. *J. Anim. Ecol.*, 70, 721–729.

Gaillard, A.J., Boutin, J., Delorme, D., Van Laere, G., Lebreton, J., Boutin, J.G.J. *et al.* (1997). Early survival in roe deer : causes and consequences of cohort variation in two contrasted populations. *Oecologia*, 112, 502–513.

Grafen, A. (1982). How not to measure inclusive fitness. *Nature*, 298, 425–426.

Grinnell, J. (1917). Field tests of theories concerning distributional control. *Am. Nat.*, 51, 115–130.

Grubb, P. & Jewell, P.A. (1974). Movement, daily activity and home range of Soay sheep. In: *Island Survivors: the Ecology of the Soay Sheep of St Kilda* (eds Jewell, P. A., Milner, C. & Boyd, J. M.). Athlone Press, London, pp. 160–164.

Gwynne, D., Milner, C. & Hormung, M. (1974). The vegetation and soils of Hirta. In: *Island Survivors: The Ecology of the Soay Sheep of St Kilda*. (eds Jewell, P.A., Milner, C., Boyd, J.M.). Athlone Press, London, pp. 36–87.

Hadfield, J.D., Richardson, D.S. & Burke, T. (2006). Towards unbiased parentage assignment: combining genetic, behavioural and spatial data in a Bayesian framework. *Mol. Ecol.*, 15, 3715–3730.

Hutchinson, G.E. (1957). Concluding Remarks. *Cold Spring Harb. Symp. Quant. Biol.*, 22, 415–427.

Jones, O.R., Pilkington, J.G. & Crawley, M.J. (2006). Distribution of a naturally fluctuating ungulate population among heterogeneous plant communities: ideal and free? *J. Anim. Ecol.*, 75, 1387–1392.

Kruuk, L.E., Clutton-Brock, T.H., Rose, K.E. & Guinness, F.E. (1999). Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proc. Biol. Sci.*, 266, 1655–1661.

MacArthur, R.H. & Pianka, E.R. (1966). On optimal use of a patchy environment. *Am. Nat.*, 100, 603–609.

McLoughlin, P.D., Boyce, M.S., Coulson, T. & Clutton-Brock, T. (2006). Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proc. Biol. Sci.*, 273, 1449–1454.

McLoughlin, P.D., Gaillard, J.M., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P. *et al.* (2007). Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology*, 88, 3192–3201.

Milner, J.M., Elston, D.A. & Albon, S.D. (1999). Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. *J. Anim. Ecol.*, 68, 1235–1247.

Morrissey, M.B., Parker, D.J., Korsten, P., Pemberton, J.M., Kruuk, L.E.B. & Wilson, A.J. (2012). The prediction of adaptive evolution?: empirical application of the secondary theorem of selection and comparison to the breeder 'S equation. *Evolution (N. Y).*, 66, 2399–2410.

Pettorelli, N. & M. Durant, S. (2007). Longevity in cheetahs: the key to success? *Oikos*, 116, 1879–1886.

Powell, R. (2000). Animal home ranges and territories and home range estimators. In: *Research Techniques in Animal Ecology: Controversies and Consequences* (eds Boitani, L. & Fuller, T. K.). Columbia University Press, New York, pp. 65–110.

Preston, B.T., Stevenson, I.R., Pemberton, J.M., Coltman, D.W. & Wilson, K. (2003). Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. *Proc. Biol. Sci.*, 270, 633–640.

R Development Core Team. (2008). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Risch, T., Michener, G. & Dobson, F. (2007). Variation in litter size: a test of hypotheses in Richardson's Ground Squirrels. *Ecology*, 88, 306–314.

Robbins, A.M., Stoinski, T., Fawcett, K. & Robbins, M.M. (2011). Lifetime reproductive success of female mountain gorillas. *Am. J. Phys. Anthropol.*, 146, 582–593.

Robinson, M.R., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M. & Kruuk, L.E.B. (2006). Live fast, die young: trade-offs between fitness components and sexually antagonistic selection on weaponry in Soay sheep. *Evolution*, 60, 2168–2181.

Servanty, S., Gaillard, J.M., Allainé, D., Brandt, S. & Baubet, E. (2007). Litter size and fetal sex ratio adjustment in a highly polytocous species: the wild boar. *Behav. Ecol.*, 18, 427–432.

Stephens, P.A., Boyd, I.L., McNamara, J.M. & Houston, A.I. (2009). Capital breeding and income breeding: their meaning, measurement, and worth. *Ecology*, 90, 2057–2068.

Stopher, K.V., Walling, C.A., Morris, A., Guinness, F.E., Clutton-Brock, T.H., Pemberton, J.M. *et al.* (2012). Shared spatial effects on quantitative genetic parameters: accounting for spatial autocorrelation and home range overlap reduces estimates of heritability in wild red deer. *Evolution (N. Y).*, 66, 2411–2426.

Tufto, J., Andersen, R. & Linnell, J. (1996). Habitat use and ecological correlates of home range size in a small cervid : the roe deer. *J. Anim. Ecol.*, 65, 715–724.

Von Holst, D., Hutzelmeyer, H., Kaetzke, P., Khaschei, M., Rödel, H. & Schrutka, H. (2002). Social rank, fecundity and lifetime reproductive success in wild European rabbits (Oryctolagus cuniculus). *Behav. Ecol. Sociobiol.*, 51, 245–254.

Williams, E.D. (1978). *Botanical Composition of the Park Grass plots at Rothamsted 1856–1976*. Rothamsted Experimental Station, Harpenden.

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Asynchrony of senescence among phenotypic traits in a wild mammal population

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ABSTRACT

The degree to which changes in lifespan are coupled to changes in senescence in different physiological systems and phenotypic traits is a central question in biogerontology. It is underpinned by deeper biological questions about whether or not senescence is a synchronised process, or whether levels of synchrony depend on species or environmental context. Understanding how natural selection shapes patterns of synchrony in senescence across physiological systems and phenotypic traits demands the longitudinal study of many phenotypes under natural conditions. Here, we examine the patterns of age-related variation in late adulthood in a wild population of Soay sheep (*Ovis aries*) that have been the subject of individual-based monitoring for thirty years. We examined twenty different phenotypic traits in both males and females, encompassing vital rates (survival and fecundity), maternal reproductive performance (offspring birth weight, birth date and survival), male rutting behaviour, home range measures, parasite burdens, and body mass. We initially quantified age-related variation in each trait having controlled for annual variation in the environment, among-individual variation and selective disappearance effects. We then standardised our age-specific trait means and tested whether age trajectories could be meaningfully grouped according to sex or the type of trait. Whilst most traits showed age-related declines in later life, we found striking levels of asynchrony both within and between the sexes. Of particular note, female fecundity and reproductive performance declined with age, but male annual reproductive success did not. We also discovered that whilst home range size and quality decline with age in females, home range size increases with age in males. Our findings highlight the complexity of phenotypic ageing under natural conditions and, along with emerging data from other wild populations and laboratory models, suggest that the long-standing hypothesis within evolutionary biology that fitness-related traits should senesce in a synchronous manner is seriously flawed.

1. Introduction

The identification of genetic and environmental manipulations that extend the lifespan of laboratory model organisms has revolutionised our understanding of the ageing process and is central to modern biogerontology (Partridge, 2010). It is becoming increasingly clear that senescent declines in health and function may begin well in advance of eventual mortality in both humans and laboratory organisms (Herndon et al., 2002; Papadopoulos et al., 2002; Christensen et al., 2009; Bansal et al., 2015). A question of growing importance, especially given the continued increase in human life expectancy, is whether interventions that extend lifespan in the laboratory also extend so-called 'healthspan', or instead leave individuals in a frail state for longer (Christensen et al., 2009; Bansal et al., 2015). A perhaps more fundamental biological question is to what degree senescence is synchronous across physiological systems and phenotypic traits in a given species (Promislow et al., 2006; Martin et al., 2007). Whilst influential evolutionary biologists have hypothesised that natural selection should shape senescence to be synchronous across physiological systems (Maynard-Smith, 1962; Williams, 1999), empirical data from humans and laboratory model organisms suggests that asynchrony is commonplace and that health- and life-span are readily uncoupled (Herndon et al., 2002; Martin et al., 2007; Christensen et al., 2009; Bansal et al., 2015). However, the benign and protected conditions experienced by laboratory model organisms and modern human societies are associated with lifespans hugely in excess of those observed under natural conditions. To understand how patterns observed in the laboratory generalise to more challenging environments and how natural selection has shaped the multifaceted process of senescence, we require studies that investigate patterns, causes and consequences of synchrony of senescence in the wild.

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Age-related declines in survival probabilities and reproductive performance are widely observed in wild vertebrates (Nussey et al., 2013). Investigation of the causes of the dramatic variation in ageing observed among species, populations and individuals in nature could offer important insights into the biology of ageing (Nussey et al., 2013; Jones et al., 2014). To date, the predominant focus of studies of senescence in the wild has been on those traits most proximate to fitness (i.e. survival and fecundity), but efforts to measure other salient phenotypic traits (e.g. body mass, secondary sexual characters, parental investment, ranging behaviour) and markers of relevant physiological processes (e.g. endocrine function, sarcopenia, oxidative stress, telomere length) are rapidly increasing (Nussey et al., 2013). Within this literature, there is mounting evidence for both differences in ageing rates between the sexes and asynchrony among phenotypic traits within sexes in the way they change with age in later life (Nussey et al., 2013). The evidence includes: reproductive cessation well before the end of life in some female mammals (Packer et al., 1998; Ward et al., 2009); evidence from a range of vertebrates for asynchrony of senescence among maternal traits associated with successful reproduction (Nussey et al., 2009; Evans et al., 2011; Massot et al., 2011; Hayward et al., 2013); asynchronous senescence among male secondary sexual traits and male reproductive performance (Nussey et al., 2009; Evans et al., 2011; Kervinen et al., 2015). Furthermore, some studies have observed so-called 'terminal declines' in traits associated with fitness, which are to some degree age-independent and occur over the period immediately preceding death (Martin and Festa-Bianchet, 2011; Nussey et al., 2011; Hammers et al., 2012). Conceivably, phenotypic traits or physiological measures could follow a progressive decline with chronological age, an age-independent and more sudden decline, or a combination of the two. Were declines with chronological age to predict phenotypic variation in later adulthood better than age-independent declines in relation to time to death, it suggests a physiological system selected to be maintained for a set period of time, with weaker selection beyond this. However, if age-independent declines provide a better fit to data than chronological age, it would suggest individual variation in the onset and rate of physiological deterioration. It should be noted, however, that age and time to death are typically confounded and their statistical separation can be challenging (Martin and Festa-Bianchet, 2011; Nussey et al., 2011). To date, few studies in the wild have directly compared the synchrony of senescence patterns among more than a handful of (typically reproductive) traits and thus the evolutionary basis of apparent asynchrony in trait senescence remains poorly understood.

Long-term, individual-based ecological studies provide detailed longitudinal data, commonly encompassing the entire lifespan of individuals, from relatively long-lived species. Survival, reproductive, behavioural, genetic, biometric and, increasingly, physiological data are routinely collected in an increasing number of studies (Nussey et al., 2013). Natural systems are obviously a great deal more variable than their laboratory counterparts, and environmental sources of mortality (e.g. predation, parasites, starvation) may mean that only a relatively small number of individuals survive to experience senescence. Furthermore, the so-called 'selective disappearance' of lower quality phenotypes can readily mask within-individual changes with age in studies in the wild (Nussey et al., 2008). Recent studies of ageing in the wild have sought to account for environmental variability and selective disappearance by statistical means or by decomposing change with age into component processes (van de Pol and Verhulst, 2006; Rebke et al., 2010). Here, we apply the former statistical approach to examine the synchrony of senescence among a wide range of phenotypic traits in an unmanaged population of Soay sheep (*Ovis aries*).

The long-term study of Soay sheep resident in the Village Bay area on the island of Hirta, St. Kilda, is one of the most detailed individual-based studies of a wild vertebrate population anywhere in the world. For three decades (1985 to present day), individuals in the population have been marked and followed from birth to death, with regular recapture of individuals, producing a wealth of information on age-specific survival, fecundity, maternal reproductive performance, male reproductive behaviour, infection with parasites, ranging behaviour, and morphology (Clutton-Brock and Pemberton, 2004). The Soay sheep on St. Kilda are unmanaged and entirely free from predation. However, they experience many environmental challenges characteristic of temperate wild vertebrate systems including over-winter food limitation, thermoregulatory challenges associated with winter weather, and infection with parasites (Clutton-Brock and Pemberton, 2004). Most mortality occurs over-winter associated with interactions among these environmental pressures, and a characteristic feature of the population is that it experiences occasional severe over-winter mortality, during which the youngest and eldest appear most susceptible (Clutton-Brock and Pemberton, 2004). Although first winter mortality can be high among lambs, individuals that survive to maturity can be long-lived: females can survive up to sixteen years (mean = 5.31 years; median = 5 years) and males to eleven years (mean = 2.67 years; median = 2 years). Phenotypic traits including body mass, parasite burdens, horn size (an important secondary sexual trait in males), and home range size and quality are all known to be associated with over-winter survival or lifetime reproductive success and are thus under natural selection in this population (Hayward et al., 2011; Morrissey et al., 2012; Johnston et al., 2013; Regan et al. in review). Separate studies of the population have documented senescence, typically from around five or six years onwards, in traits including annual survival and fecundity, body mass, parasite burden, and maternal reproductive performance traits (Robinson et al., 2006; Hayward et al., 2009; Nussey et al., 2011; Colchero and Clark, 2012; Hayward et al., 2013), but no direct comparison of senescence patterns among sexes or traits has been made. Furthermore, whilst a previous study of the population found evidence that female body mass follows a pattern of terminal decline rather than a progressive decline with age (Nussey et al., 2011), broader comparisons of such patterns among other traits have not yet been made.

Here, we undertake analyses of age-related variation in twenty different traits measured in males and females during later adulthood. Our principal aims are: (1) to determine whether age-related variation is best-explained by changes with chronological age or by changes associated with time-to-death, and (2) to statistically compare ageing trajectories among functionally-linked groups of traits in order to determine the extent to which ageing rates are synchronous among traits. Available evolutionary theory predicts synchrony of senescence in fitness-related traits (Maynard-Smith, 1962), whilst empirical data on wild populations published to date suggests that some degree of synchrony is usually observed (Nussey et al., 2009; Evans et al., 2011; Massot et al., 2011; Hayward et al., 2013).

2. Materials and methods

2.1. Study population and data collection

Soay sheep are descendants of domestic sheep that were present throughout northwest Europe during the Bronze age, and probably reached the St. Kilda archipelago 3000–4000 years ago (Clutton-Brock and Pemberton, 2004). A population has lived on the island of Soay since their arrival on the archipelago, but there is compelling evidence that they interbred with the now extinct dunface breed (a precursor of modern blackface sheep) sometime in the mid-nineteenth century (Feulner et al., 2013). The largest island of the archipelago, Hirta (638 ha), was evacuated of its indigenous human population and their modern domestic stock in 1930. In 1932, 107 Soay sheep were reintroduced to the island from the neighbouring island of Soay, following which they increased to carrying capacity and have since remained unmanaged. Monitoring of the population began in 1959. Since then, there have been two periods of intensive study in the Village Bay area: 1959 to 1968 (Jewell et al., 1974) and 1985 to the present (Clutton-Brock and Pemberton, 2004). Our study uses field data collected during

this latter period of intensive, individual-based study of the Village Bay population, which has followed a standardised annual routine of data and sample collection.

The Village Bay study area is 170 ha, and contains approximately 30% of the total island sheep population. Three times per year (February–March, July–August, and October–December), ten censuses of the study area are carried out, during which the locations of all individuals are recorded (Clutton-Brock and Pemberton, 2004). Females give birth in spring (March–April) and on average around 13% of litters are twins, the remainder being singletons. Soay lambs develop rapidly and are typically weaned by mid-June, although they may continue to be suckled throughout the summer. Around 90% of lambs born in the Village Bay study area are caught within a few days of birth, tagged for future identification, weighed and blood and tissue sampled for genetic analysis. Daily monitoring of the population during the spring means that the day of birth of these lambs is known precisely. Each August, as many sheep from the study population as possible (usually 50–60%) are rounded up in a series of temporary traps, caught and processed over the course of a two week period. Previously unknown individuals are tagged and captured individuals have a variety of measures taken including body weight, hind and foreleg lengths, horn lengths, circumference and growth and testes circumference in males. Faecal samples are taken whenever possible and a variety of parasite egg counts are made (see below for details). During the rut (October to November) males compete for access to females as they come into oestrus and the study area is monitored daily and the identities of each ram and ewe in consort are noted. Most mortality occurs during the winter months, and regular censuses and mortality searches during the winter months mean that the carcasses of most over-winter mortalities are found and death dates can be assigned with confidence to most animals (Clutton-Brock and Pemberton, 2004).

2.2. Phenotypic traits

From the current Soay sheep database we identified twenty phenotypic traits for further investigation (Table 1). The traits were divided into six classes: vital rates (annual survival, male annual reproductive success and two traits underpinning female annual reproductive success); biometric measures (7 traits); parasitological measures (3 traits); home range measures (2 traits); maternal performance (3 traits); rut behaviour (1 trait). Each of these traits was measured longitudinally in every individual in each year where available. The traits are defined in detail within these classes below.

We calculated age based on an approximate 'sheep year' running from May through to April rather than using a calendar year. Thus, a sheep born in year t (typically in March or April of that year) was assigned to age zero for all traits measured between May in year t and the end of April in year $t+1$, including all reproductive traits associated with its reproduction in the spring of year $t+1$. This is described below, and details of the timing of trait collection are also presented in Table 1. We restricted our data selection to individuals that were known to have died of natural causes between 1985 and 2014 inclusive, and which had a known birth year. Trait measures were also restricted to the time period of 1985–2014 inclusive, although not all measures were available from 1985 (see Table 2 for more details).

Previously studies suggest that the Soay sheep have largely stopped growing and showing signs of improvement in fitness-related traits by the age of three or four, and there is little evidence for senescence beginning before five or six years of age in any trait (Colchero and Clark, 2012; Hayward et al., 2013). We therefore decided to investigate senescence patterns from age four onwards. Since very few females or males survived or were measured beyond thirteen and nine years of age, respectively, we grouped measurements from these ages onwards into a single final age class ('13' for females and '9' for males, consisting of <10% of individuals in both sexes). We also calculated 'years until death' for each trait (as the difference in years between an animal's longevity and its current age) and found that, when considering only measures from ages four or more, there were very few observations in females or males beyond eight and four years from death, respectively. We therefore grouped observations at or beyond these years until death into a final class. The final numbers of measurements and individuals measured for each trait available are presented in Table 2.

2.2.1. Vital rates

Survival: available data on individual birth and death date was used to construct an individual life-history for each animal. Thus, each animal was represented by as many data records as the number of years in which they were observed to be alive. Survival was monitored for an individual alive in April of year t to May 1st of year $t+1$, with survival of that period coded 1 and death coded 0.

Female fecundity and twinning: Female fecundity was coded 1 if a female gave birth in that sheep year and 0 if she did not (see Table 1);

Table 1
Schematic of Soay sheep annual cycle and timing of data collection, with respect to an individual's age.

Calendar year	*t*								*t+1*														*t+2*			
Month	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A
Measures								**Mortality**				**Male reproductive success**												
	Home range size & quality																							
				Biometrics		**Rut**							**Female reproductive success**											
						Number of consorts																		
				Weight									Fecund/barren											
				Foreleg length									Singleton/twin											
				Hindleg length									**Maternal performance**											
				Testes circumference									Date of birth											
				Horn length									Offspring birth weight											
				Horn circumference									Offspring first winter survival											
				Horn growth																				
				Parasites																				
				Faecal Strongyle egg count																				
				Faecal Coccidia oocyst count																				
				Ked count																				

Table 2
List of phenotypic traits for which GLMMs were run, with units, sample sizes and details of error distribution used. See Figure S1 for plotted trait distributions.

Trait	Units	Season of measurement	Sex	Years available	Sample size (individuals)	Error distribution
Vital rates						
Annual survival[a]	Yes/no	Annual	Both	1985–2014	3223 (821)	Binomial
Female fecundity	Yes/no	Spring	F	1985–2014	2662 (593)	Binomial
Female twinning rate	Yes/no	Spring	F	1985–2013	1778 (479)	Binomial
Male ARS	No. of offspring	Spring	M	1987–2014	411 (176)	Poisson
Biometric						
Weight	kg	August	Both	1985–2014	1394 (559)	Normal
Foreleg length	mm	August	Both	1988–2014	1238 (486)	Normal
Hind leg length	mm	August	Both	1988–2014	1297 (494)	Normal
Testes circumference	mm	August	M	1985–2014	135 (78)	Normal
Horn length	mm	August	M	1985–2014	133 (73)	Normal
Horn circumference	mm	August	M	1989–2014	128 (67)	Normal
Horn growth	mm	August	M	1988–2014	118 (64)	Normal
Parasitology						
Ked count	Number	August	Both	1988–2014	1294 (493)	Poisson
FEC[b]	Eggs/g	August	Both	1988–2014	1230 (485)	Poisson
FOC[b]	Oocysts/g	August	Both	1993–2014	1089 (442)	Poisson
Maternal traits						
Offspring survival[c]	Yes/no	Annual	F	1985–2014	1772 (468)	Binomial
Date of birth[c]	Days since 1st March	Spring	F	1985–2014	1912 (471)	Normal
Offspring weight at birth[d]	kg	Spring	F	1985–2014	1704 (459)	Normal
Male reproductive behaviour						
Number of consorts	Rut census observations	Rut	M	1987–2014	411 (176)	Normal
Home range behaviour						
Home range size	Ha	Annual	Both	1985–2014	2646 (658)	Normal
Home range quality	% cover *Holcus*	Annual	Both	1985–2014	2646 (658)	Normal

[a] Individual identity and longevity not included in model.
[b] Observation included as random effect in model.
[c] Offspring sex and twin status included as fixed effects in model.
[d] Capture age in days, offspring sex and twin status included as fixed effects in model.

female twinning rate was only scored for females which gave birth and was coded 1 if the female had twins and 0 if she had a singleton.

Male annual reproductive success (*ARS*): the number of paternities assigned to a male in a given year. Only males observed during rut censuses in a given year (observed at least once in a census between October and November) were included as potentially having any ARS at a given age. Paternities were assigned based on genotyping individuals at 315 SNPs in the program MasterBayes (Hadfield et al., 2006) and using 14–18 microsatellite loci (Overall et al., 2005). This method was able to infer paternity for 4593 individuals in the study population (for more details see Bérénos et al., 2014).

2.2.2. Biometric measures

Body weight (*kg*): measured to the nearest 0.1 kg at capture in August.

Leg measurements (*mm*): foreleg length was measured to the nearest mm as the length of the metacarpal with hoof and knee joint bent away from it; hind leg length was measured in mm from the tubercalcis of the fibular tarsal bone to the distal end of the metatarsus (Milner et al., 1999).

Horn measurements (*mm*): horn length was measured from the base of the horn, along the outer curvature to the tip; horn circumference was measured around the base of the horn at the point closest to the skull; horn growth was measured from the base of the skull, along the outer curvature to the first growth increment (Johnston et al., 2013). Only data from normal-horned males were included.

Testicular circumference (*mm*) was measured at the widest point of the scrotum as a proxy for testes mass (Preston et al., 2012).

2.3. Parasitological measures

Strongyle faecal egg count (*FEC*): estimated as the number of strongyle nematode eggs present per gramme of faeces collected in the August of year *t* using a modified McMaster egg counting technique (described in Craig et al. (2006)). Faecal egg counts were grouped into bins of 100 and counts >1000 were collapsed into the highest bin (around 1% of samples). This is a combined count for five strongyle species which have eggs indistinguishable by eye (Gulland and Fox, 1992).

Coccidian faecal oocyst count (*FOC*): was estimated as the number of oocysts present per gramme of faeces, using the modified McMaster method. Coccidia are protozoan parasites, consisting of 13 species which occur at high prevalence in the population, but with oocytes of indistinguishable morphology which are grouped into one count of FOC (Craig et al., 2007). Faecal oocyst counts were grouped into bins of 100 and counts >2000 were collapsed into the highest bin (around 3% of samples).

Ked count: the number of live keds (*Melophagus ovina*) counted during a one-minute search of the wool on a sheep's belly performed at capture in August. Keds are wingless ectoparasitic flies that live on the wool of the sheep and are blood feeders and can be observed in large numbers on young animals in some years (Clutton-Brock and Pemberton, 2004).

Faecal egg counts for other parasites, including the nematodes *Nematodirus* spp., *Capillaria longipes* and *Trichuris ovis*, and the cestode *Moniezia expansa* were also undertaken (Craig et al., 2008), but lacked sufficient prevalence or abundance in adults to permit meaningful analyses.

2.3.1. Home range measures

Home range size (hectares) and *home range quality* were calculated as follows. Briefly, census locations for each sheep at each age (May in year *t* to April in year $t + 1$) were collated and animals with fewer than ten census observations at a given age were excluded from further analyses. 70% kernel home ranges were calculated using the package 'adehabitatHR' (Calenge, 2006), and home range size was calculated in hectares. Based on the Ordnance Survey Grid, the study area was

divided into 160 one hectare squares (100 m × 100 m). Between the years of 2008 and 2012, complete species lists were compiled for the vascular plants present in each hectare, and the percentage cover of each species was scored by eye (to the nearest 5%). Mean percentage covers of plant species were calculated for each individual by determining the hectares contained within the home range, extracting the vegetation cover in each hectare and weighting by the proportion of the hectare that was within the home range. *Holcus lanatus* was selected to represent high quality plant communities, based on previous studies of vegetation preferences and a separate principal components analysis (PCA) which included the fourteen most abundant plant species (Regan et al. in review). Home range quality was calculated as the proportion of *H. lanatus* cover within an individual's home range.

2.3.2. Rut behaviour

Number of rut consorts: Soay sheep have a highly promiscuous mating system in which females are observed to mate with many males during a 1–4 day oestrus period (Clutton-Brock and Pemberton, 2004). Male Soays exhibit mate-guarding behaviour (consorting) in order to block access to a female in oestrus by other males. Consorts were defined as a close spatial relationship between a male and female (typically within 5 m), with frequent courtship and attempted defence of the ewe by the ram (Preston et al., 2001). Daily observations were made during the rut period and the identities of males and females in consort were noted. We calculated the total number of times a male was observed in consort over the course of a rut from these observations. Note that whilst the number of consorts has been shown to be correlated with the number of paternities a male is subsequently assigned through genotyping, consort censuses have rather poor predictive power for male ARS (Coltman et al., 1999a).

2.3.3. Maternal performance

Date of lamb birth: the number of days after March 1st in year $t + 1$ on which a female gave birth. As with all maternal performance traits, the unit of analysis was the lamb, rather than the mother: thus twin lambs both received a separate data record.

Birth weight (*kg*): the weight, measured to the nearest 0.05 kg, of the lamb born in year $t + 1$ upon its first capture, which was within a week of birth in 95% of cases.

Offspring survival: whether the lamb born in year $t + 1$ (contributing to maternal performance at age t) survived to May 1st in year $t + 2$.

2.4. Statistical analyses

All analyses were performed using R version 3.2.0 (R Core Team 2012).

2.4.1. Generalised linear mixed-effects models: mapping age-related changes in phenotype

We began by examining the distributions of all phenotypic traits in both sexes (Fig. S1). Home range area and the number of rut consorts were both right-skewed and so were log transformed and then assumed to be normally distributed in further analyses. We initially sought to calculate age-specific predictions for each trait in both males and females (where appropriate), whilst accounting for individual and annual variation and selective disappearance effects. We followed the approach used in a previous study of senescence in different reproductive traits in wild red deer (Nussey et al., 2009). We constructed generalised linear mixed-effects models (GLMMs) for each trait using the package 'lme4' (Bates et al., 2014). All models included individual identity and year of measurement as random effects to account for variation among individuals and years, except survival for which individual identity was excluded (as death is observed only once per individual). In models of faecal egg count (FEC) and faecal oocyst count (FOC), we fitted GLMMs with a Poisson error distribution which also included an observation-level random effect to account for over-dispersion (following Elston et al., 2001). In all models, we included linear and quadratic terms for individual longevity as covariates, to account for covariance between lifespan and trait value ('selective disappearance', van de Pol and Verhulst, 2006). Additional fixed effects terms were included in maternal performance traits models. Sex of offspring and whether the offspring were twins or singletons were included as categorical fixed effects in all models, since both of these variables are known to affect lamb birth date, birth weight and survival (Wilson et al., 2005), whilst the capture age in days was included as a continuous covariate in the model of offspring birth weight, since lambs are not all captured on the same day after birth and they grow rapidly. Full details of the sample sizes and error structures used for each trait are presented in Table 2.

For each trait, we fitted and compared up to seven different GLMMs to determine whether variation in the trait was better explained by chronological age or years remaining until death and, where appropriate, whether rates of change in relation to these two variables differed between the sexes. Our 'null' model with respect to senescence included all fixed and random terms described above but excluded age and years remaining until death. We then fitted further models describing age-specific change in different ways. Firstly, with individual age as a categorical fixed effect, allowing the trait mean to vary independently across all ages. Then, in traits measured in both sexes (see Table 2) we also included a categorical fixed effect of sex (trait means differ between sexes but age trajectories are identical) and an age-by-sex interaction (age trajectories can differ among the sexes). We also fitted models with years-to-death as a fixed factor (instead of age), to test for variation in the trait associated with age-independent loss-of-function. Again, where the trait was measured in both sexes, we included sex as a fixed categorical variable and a sex-by-age interaction. Age and years-to-death were fitted as categorical fixed effects rather than continuous covariates because our aim was to generate age-specific estimates and standard errors for each trait in order to compare them; fitting age and years-to-death as covariates would have required using a specific functional form (e.g. linear, quadratic) and not allowed us to generate age-specific standard errors. We compared the fit of the models for each trait using Akaike Information Criterion (AIC). We then extracted the predicted means and standard errors for each age and year-before-death, after controlling for the other fixed and random effects, using the package 'lsmeans' version 2.17 (Lenth and Hervé, 2014).

Years remaining until death was not fitted in survival models because it is perfectly correlated with survival. It was also not fitted in models of female breeding success, twinning or maternal traits. Due to the way we structured our 'sheep year' (Table 1), females almost invariably fail to reproduce in their final year of life, simply because the vast majority die over the winter preceding their 'last' lambing season. As a result, we could not construct models including years to death that were directly comparable to other traits for these maternal reproductive performance measures.

2.4.2. Generalised additive models: testing for synchrony of senescence among traits

Variation in most traits was best described by age, rather than years to death (see Results) so we focussed examination of synchrony of senescence on predictions from our GLMMs including age as a categorical fixed effect. Where the trait was measured in both sexes, we used predictions from models with a sex-by-age interaction to predict age-dependent variation in both sexes. We only tested for asynchrony among traits which showed a significant change with age in the GLMMs (omitting foreleg length, ked count, FOC, female twinning and male consorts; see Results). We applied generalised additive models (GAMs) to the age-specific predictions of the remaining traits from our GLMMs to test whether groups of traits identified a priori, showed similar or different senescence patterns (following Nussey et al., 2009). GAMs fit non-parametric smoothing functions relating a trait to a covariate (in this case, age) and allow comparison of trajectories among groups of variables without the need to assume that traits all

follow a particular function with respect to senescence (e.g. quadratic or higher order polynomial function).

Lower birth dates (when expressed in Julian days since 1st March) and strongyle faecal egg counts are associated with higher fitness (Wilson et al., 2005; Hayward et al., 2011), unlike other traits which would be expected to show positive associations with fitness. To ensure that all age-related changes were in the same direction with respect to fitness and function, we made the predicted values of birth dates and egg counts negative prior to further analysis. The age-specific predicted means of all traits were then standardised to be on comparable scales by subtracting the age-specific predicted mean at age 4 for each sex from the age-specific predicted mean at each age and then dividing this by the range of age-specific predicted means from age 4 to 13 in females and 4 to 9 in males. We then fitted GAMs through these standardised trait values: the value at age 4 was zero for each trait for each sex. Our standardized age-specific predictions were weighted by the inverse of the age-specific standard error from the appropriate trait GLMMs to ensure greater weight to the (younger) ages for which more data were available.

Our aim was to determine whether all traits showed synchrony of senescence, whether each trait in each sex showed distinct senescence trajectories ('total asynchrony'), or whether the senescence trajectories among traits could be grouped based on physiological or ecological similarities or between the sexes (various forms of 'partial asynchrony'). We hypothesised nine potential heterochrony groupings among the 15 remaining traits, and also fitted a 'null' age model which did not include any age term and a model which fitted a single age function to all traits ('total synchrony'). The details of the trait groupings for the nine heterochrony models are presented in Table 4. The response variable in these comprised all age-specific predictions from all traits, with explanatory variables coding either the age or the group of that trait in each model. For instance, in the model of 'total synchrony' all traits belonged to the same group and an identical age function was fitted to all traits whilst in the 'total asynchrony' model each trait belonged to a different group and thus had a potentially distinct age function fitted. For each of the heterochrony models, we fitted separate models where: (1) the intercept associated with the grouping varied (only the mean at age 4 differed among groups, the senescence trajectory was the same); (2) the senescence trajectory associated with the grouping varied (senescence trajectories varied among groups but the mean at age 4 did not); (3) both the intercept and senescence trajectory associated with the grouping varied (both mean at age 4 and senescence trajectories varied among groups). The best-fitting model was determined by selecting the model with the lowest AIC value.

3. Results

Most traits showed strong age-dependence in later adulthood (Fig. 1), and in the majority of traits chronological age explained trait variation better than the number of years remaining until death (Table 3), indicating that trait variation was largely better-explained by current age rather than remaining lifespan. Five of our 20 phenotypic traits did not show any evidence of age-dependence from four years of age onwards: foreleg length, ked count, FOC, female twinning rate and male rut consorts (Table 3). Many of the ageing patterns observed recapitulate those observed in previous studies of this system, including: (i) declining survival probability in both sexes from 5–6 years onwards (Colchero and Clark, 2012); (ii) declines in female fecundity, offspring birth weight and offspring survival with maternal age but not in female twinning rate (Hayward et al., 2013); (iii) strongyle FEC increased with age in later life in both males and females (Hayward et al., 2009); and (iv) August weight in females declined in old age (Nussey et al., 2011). That said, the GLMMs also revealed many novel aspects of the ageing process in the Soay sheep. Male ARS showed no sign at all of declining at later ages, instead increasing up to around seven years of age and remaining at around 2 offspring per year on average until the eldest age class (Fig. 1). This increasing trend was accompanied by an evident decrease in testes circumference and body mass in males (Fig. 1). Horn morphology in males showed a complex pattern of variation with age: total horn length increased, which is not surprising given that each year a new horn increment is grown; but horn circumference decreased whilst our measure of annual horn growth (length of the most recently grown horn increment) varied with age without showing an obvious trend (Fig. 1).

Of the nine traits which were measured in both sexes, three showed no change with age in either sex (FOC, ked count, foreleg length). There was no statistical support for an interaction between sex and age in survival or FEC, suggesting similar rates of decline and increase, respectively, in males and females (Table 3, Fig. 1). However, there was strong support for models including sex-by-age interactions for weight, home range size and home range quality (Table 3). Male weight increased with age until six years old and then declined thereafter, whilst female weights remained stable until around 10 years of age before declining (Fig. 1). Home range size declined with age in females but actually increased from seven years onwards in males, whilst home range quality appeared to decline in very late life (from 11 years onwards) in females but increased slightly with age in males (Fig. 1).

Only two traits were better fitted by years until death than chronological age: weight and hind leg length (Table 3, Fig. 2). There was a dramatic decline in weight of around 1 kg across the two years preceding death in females, a finding that has been documented before in this system (Nussey et al., 2011). However, males also showed this pattern, losing around 2 kg on average across the two years prior to death (Fig. 2). Hind leg length showed little evidence of change with respect to either age or years to death in females, but in males slight decreases were evident over the years preceding death (Fig. 2). Since only these two traits showed compelling evidence for age-independent declines in later life, we proceeded to focus on testing whether or not particular groups of traits followed different trajectories with chronological age in later life.

Further analyses supported the presence of considerable and complex asynchrony of senescence both between sexes and among traits within sexes (Table 4, Fig. 3). The best supported model of senescence was the most complex, involving separate age functions for every trait in each sex (Table 4), and this model outperformed the next best by a considerable margin (AIC difference of 83.59). Models with either a single age function for all traits (synchrony of senescence) or separate functions for each sex performed extremely poorly (respective $\Delta AIC = 232.18$ and 233.01 compared to the total asynchrony model).

4. Discussion

Our analyses constitute the broadest assessment of longitudinal phenotypic changes in later life so far conducted in a wild organism. The results highlight both the complexity and asynchrony of changes occurring during the senescent phase of life in both males and females in our study population. Our models clearly show that senescence trajectories across different traits are highly divergent and cannot be readily simplified or grouped (Table 4, Fig. 3). Previous studies of natural populations have documented apparent differences in patterns of senescence among phenotypic traits in birds, mammals and reptiles (e.g. Nussey et al., 2009; Lecomte et al., 2010; Evans et al., 2011; Massot et al., 2011). Studies of model organisms, notably nematode worms, also point to variability in ageing rates among different physiological systems and health measures (e.g. Herndon et al., 2002; Bansal et al., 2015). Although the present study and this previous research supports the idea that ageing is asynchronous across physiological systems and phenotypes, understanding both the generality and the evolutionary causes of asynchrony in senescence remains an important challenge within both evolutionary ecology and bio-gerontology.

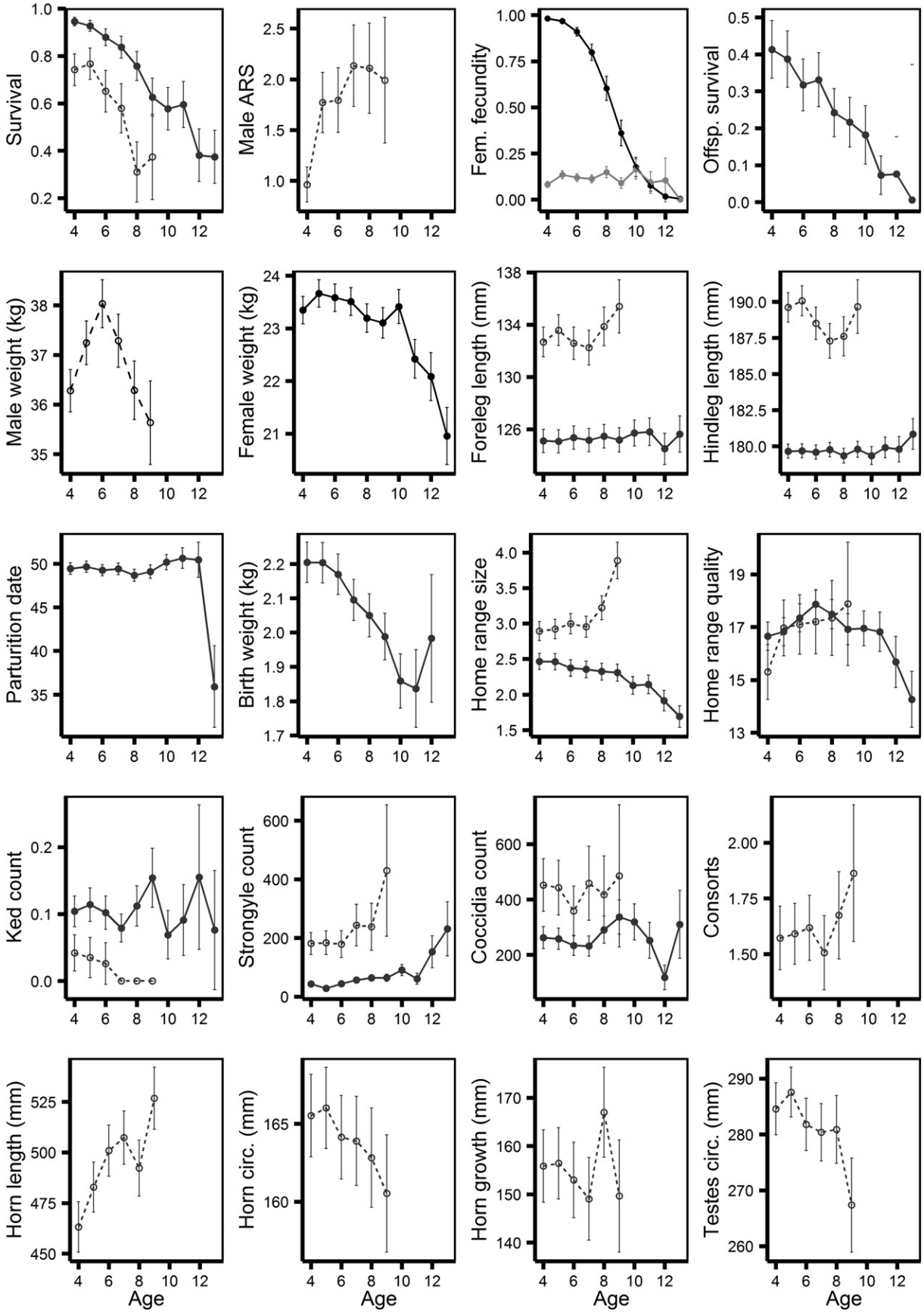

Fig. 1. Age-dependent variation in twenty traits measured in wild Soay sheep. Points and bars are means and standard errors estimated from generalised linear mixed models (see text and Table 2 for details), with females represented by solid lines and symbols, and males represented by broken lines and open symbols. In the "Fem. Fecundity" plot, the probability of a female giving birth at a given age is plotted in black, and the probability of her twinning (given that she reproduced) is plotted in grey. Note that male and female weight predictions are plotted separately to allow age trends to be clearly visualised given that males are much heavier than females. Units are given in the main text.

Table 3
Table of AIC values comparing generalised linear mixed-effects models of each trait which included no age or years to death term ("Null"); either age as a fixed factor or years until death (YTD) as a fixed factor, plus sex as a fixed factor where the trait was measured in both sexes; and an interaction between either age or years until death and sex, where the trait was measured in both sexes. The model best explaining variation in the trait (i.e. the lowest AIC value, unless a simpler model has an AIC value which is less than 2 higher than that of the best model) is highlighted in bold italics.

Trait	AIC value						
	Null	Age	Age + sex	Age * sex	YTD	YTD + sex	YTD * sex
Survival	2863.117	2715.22	***2592.656***	2599.343	NA	NA	NA
Weight	6074.058	6816.51	6039.261	6031.031	6814.792	6028.522	***6018.787***
Foreleg length	***7151.253***	7284.47	7162.22	7157.373	7279.416	7157.146	7155.941
Hind leg length	7602.844	7719.81	7614.598	7605.329	7718.115	7612.775	***7598.902***
Testes circumference	1173.119	***1151.13***	NA	NA	1156.124	NA	NA
Horn length	1398.316	***1328.52***	NA	NA	1354.046	NA	NA
Horn circumference	926.045	***916.88***	NA	NA	919.1126	NA	NA
Horn growth	1114.24	***1091.05***	NA	NA	1100.489	NA	NA
Keds	***1093.488***	1114.93	1105.941	1113.032	1109.181	1101.437	1103.797
Faecal strongyle egg count	3426.779	3504.26	***3394.422***	3400.567	3510.888	3402.721	3404.63
Faecal Coccidia oocyst count	***5637.975***	5658.64	5641.37	5650.53	5652.877	5636.516	5639.961
Home range area	4809.752	4825.97	4779.724	***4767.779***	4833.229	4786.812	4791.489
Home range quality	16955.24	16939.14	16938.923	***16934.192***	16964.77	16964.578	16960.905
Female fecundity	2950.807	***2296.43***	NA	NA	NA	NA	NA
Female twinning rate	***1654.162***	1660.27	NA	NA	NA	NA	NA
Offspring date of birth	11800.82	***11790.19***	NA	NA	NA	NA	NA
Offspring birth weight	1977.585	***1966.58***	NA	NA	NA	NA	NA
Offspring first year survival	1764.19	***1756.36***	NA	NA	NA	NA	NA
Male annual reproductive success	1702.948	***1663.91***	NA	NA	1682.089	NA	NA
Male rut consorts	***1030.405***	1049.155	NA	NA	1043.943	NA	NA

4.1. Asynchrony and evolutionary theories of ageing

The existing body of work on the evolutionary theory of ageing currently offers little to help our understanding of among trait asynchrony in ageing rates within populations. Available theory that specifically addresses this issue appears to consist of a verbal model that argues for synchronous senescence arising as a consequence of natural selection. This model – first suggested by Maynard-Smith (1962) and reiterated by Williams (1999) – imagines that each trait has some critical lower value below which death occurs. Under this model, the intensity of selection for a trait increases as its mean value across the population decreases. As a consequence, a trait with a mean value that is closest to its critical threshold relative to other traits will experience the strongest selection for improvement. Conversely, trait means that are furthest above the threshold are under the weakest selection to improve. Selection against mortality declines with age, and it follows that age-specific trait values will decline with age as well. However, Maynard Smith's model argues that natural selection favours a situation in which all traits evolve to the same trait values relative to their specific critical thresholds. As a result, Maynard Smith argued that all survival-related traits should senesce at the same rate.

As discussed above, available empirical evidence suggests that Maynard Smith's prediction, and therefore the model's assumptions about how natural selection acts on senescence across traits, are wrong. Although never formalised mathematically, the model appears to rest on a form of threshold selection, in which individuals with values below some critical point have one fitness value and those above that threshold have another (Falconer and Mackay, 1996). Although such threshold relationships may exist, we hypothesise that few continuously varying physiological processes or phenotypic traits actually relate

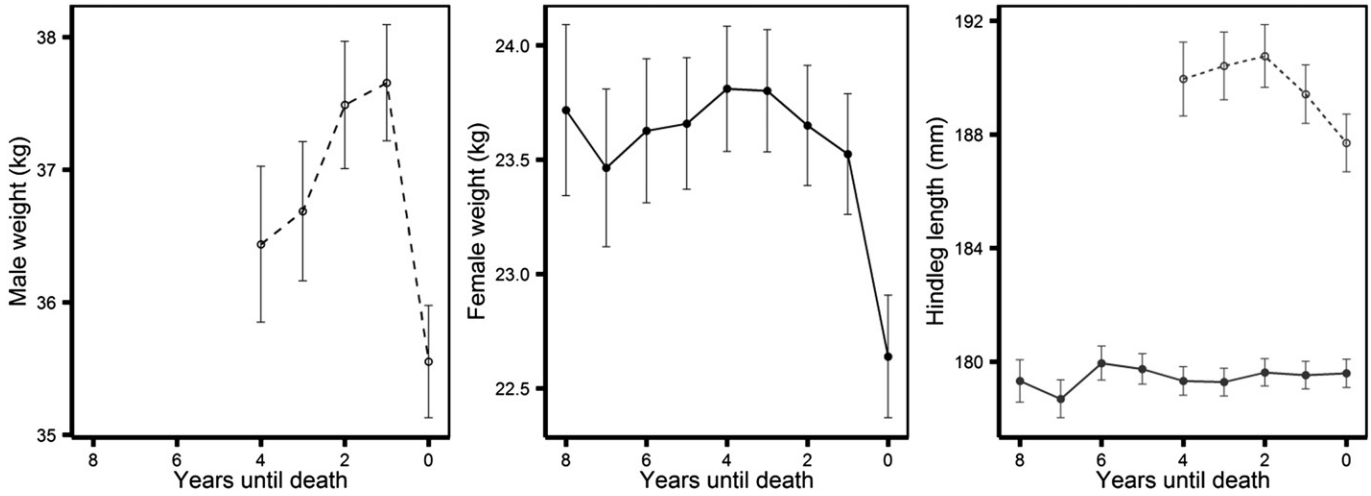

Fig. 2. Two morphometric traits (weight and hind leg length) for which years remaining until death explained more variation in our models than chronological age, plotted against years to death. Females are represented with solid lines and symbols and males are represented by broken lines and open symbols (with the sexes plotted separately for weight as in Fig. 1). Points and error bars are predicted means and standard errors from GLMMs including years to death as a factor along with its interaction with sex. Units are given in the main text.

Table 4
A comparison of 11 different models of the senescence trajectories of phenotypic traits in wild Soay sheep. The first two models are the null model with respect to senescence and the model of synchrony of senescence, under which all traits follow the same trajectory. The remaining 9 models encompass different scenarios of heterochrony. For each model AIC values are presented, and for each heterochrony model three variant models were fitted, for which only the intercept or the age trajectory alone varied among groups, or for which both were allowed to vary. The model with the lowest AIC is the best fitting and is denoted in bold with grey fill.

		AIC value		
Trait grouping	Number of groups	Intercept only	Senescence only	Intercept + senescence
No age function	0	415.96	NA	NA
Same age function for all traits	1	227.50	NA	NA
One trajectory for each sex, same trajectory for traits within sexes	2	220.77	221.09	218.34
Group 1: Female fecundity, maternal performance, male ARS, testicular circumference, horn measures Group 2: All other traits	2	222.85	228.43	218.43
Group 1: Biometric traits Group 2: Vital rates, maternal performance Group 3: Parasitological traits Group 4: Home range traits	4	199.08	223.15	182.25
Group 1: Vital rates Group 2: Maternal performance traits Group 3: Biometric traits Group 4: Parasitological traits Group 5: Home range traits	5	200.66	223.79	185.66
Group 1 & 2: Biometric traits by sex Group 3: Female vital rates & maternal performance Group 4: Male vital rates Group 5 & 6: Parasitological traits by sex Group 7 & 8: Home range traits by sex	8	198.18	209.93	171.11
Group 1 & 2: Vital rates by sex Group 3: Maternal performance traits Group 4 & 5: Biometric traits by sex Group 6 & 7: Parasitological traits by sex Group 8 & 9: Home range traits by sex	9	200.1	210.98	174.6
Group 1 & 2: Survival by sex Group 3 & 4: Fecundity / ARS by sex Group 5: Maternal performance traits Group 6 &7: Biometric traits by sex Group 8 & 9: Parasitological traits by sex Group 10 & 11: Home range traits by sex	11	164.55	1 57.72	78.91
Different age function for all traits, but for traits measured in both sexes the sexes share a trajectory	15	166.07	190.73	95.41
Different age function for all traits and sexes	21	159.57	152.01	**-4.68**

to age-specific survival in this way. It seems more likely to us that a unit of trait decline will confer some proportional increase in risk of mortality or decrease in reproductive performance. Furthermore, Maynard Smith's model considers only trait relationships with survival, neglecting equally important and potentially even more complex relationships with fecundity and reproductive performance. To develop more nuanced evolutionary predictions regarding trait synchrony, we require a better understanding of whether and how age-specific selection gradients differ among phenotypic traits. These relationships are readily obtained using classical phenotypic selection and demographic methods (e.g., Lande and Arnold, 1983; Moorad, 2014), and estimating variation in age-dependent selection across traits represents an important next step for studies of ageing in the wild. It will be similarly important to develop our understanding of the quantitative genetic relationships among traits at different ages in wild animals. Genetic correlations among traits in late life, or indeed in earlier life when selection is much stronger, may constrain or facilitate the evolution of asynchrony in senescence rates in response to prevailing selection pressures. Although age-specific genetic covariance matrices among traits have been estimated in laboratory model systems (e.g. Tatar et al., 1996), we are not aware of any such estimates from the wild (Charmantier et al., 2014).

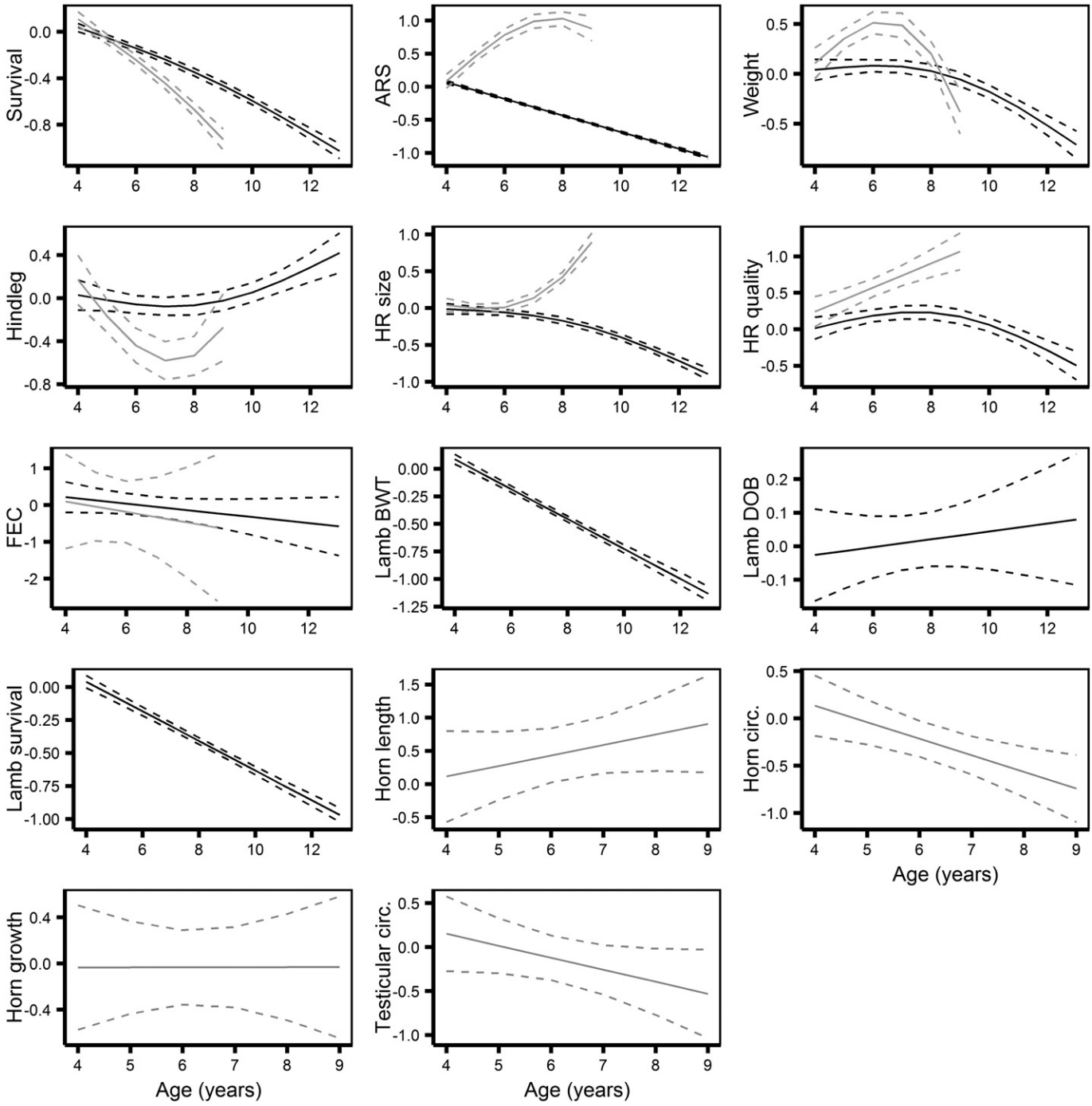

Fig. 3. Predictions from the best-fitting generalised additive model (see Table 4) which supported total synchrony with all traits measured followed a different ageing trajectory in males and females. Solid lines show predicted trait values across age; broken lines show predicted standard errors. Black lines represent traits measured in females and grey lines represent traits measured in males. Abbreviations are as follows: ARS — annual reproductive success; FEC — faecal egg count; HR size — home range size; HR quality — home range quality; Lamb BWT — lamb birth weight; Lamb DOB — lamb date of birth.

Although Maynard Smith's verbal model predicting synchrony of senescence appears over-simplistic and is contradicted by available empirical evidence, evolutionary genetic theory can provide explanations and predictions regarding observed patterns of asynchrony in ageing rates. The challenge is to obtain the required estimates of age-specific selection gradients and age-dependent genetic covariance matrices among traits in order to parameterise evolutionary models. This is no small challenge, as these require both detailed information on the relatedness structure of the population and very large sample sizes. However, the Soay sheep system, with its SNP-based pedigree and detailed longitudinal records for a wide range of phenotypes and fitness estimates (Bérénos et al., 2014, 2015) is one of several wild systems where this may be possible.

4.2. Sex differences in senescence

Our analyses have revealed hitherto unappreciated differences in senescence patterns between the sexes in the Soay sheep of St. Kilda. Sex differences in senescence are predicted by evolutionary theory for polygynous species in which males tend to have shorter life expectancies than females (Williams, 1957; Bonduriansky et al., 2008). Specifically, males are predicted to senesce earlier and faster in such systems either

because selection weakens more strongly with age or because costs of reproduction are greater in males (Bonduriansky et al., 2008). Comparative studies offer some support for this prediction (Clutton-Brock and Isvaran, 2007) and studies of other species of ungulate suggest that males show earlier or stronger declines in survival probability, body mass and annual fecundity (Mysterud et al., 2001; Toigo et al., 2007; Nussey et al., 2009). However, although males had lower average survival probability than females in later adulthood, we found no evidence for differences in the ageing pattern in later life, a finding corroborated by a previous Bayesian mark-recapture analysis in this population (Colchero and Clark, 2012). More surprisingly, whilst female fecundity and key maternal reproductive performance parameters (offspring birth weight and survival) declined approximately linearly with age, male annual reproductive success increased and then plateaued, but did not decline with age. This result is at odds with previous studies, which suggested declines in male ARS from 6 or 7 years onwards (Coltman et al., 1999b; Robinson et al., 2006). However, these studies used less well resolved, microsatellite-based pedigrees and at least a decade's less data. In both studies, the apparent decline in ARS in very old males is based on very small samples and was not directly shown to be statistically significant. Our analyses, based on a larger sample size and a more complete pedigree, suggests that there is no evidence for a decline in male ARS in very old age in this population.

Our analyses do offer evidence that males are senescing, however. Testes size declined with age, a result mirrored in previous study suggesting that testosterone levels during the annual rut also decline from around 4 years onwards (Preston et al., 2012). More strikingly, males lost on average 2 kg over the two summers before they died (around 5% of average body mass at four years of age), almost double the comparable loss documented here and previously in females (Nussey et al., 2011; note that females are around 35% lighter than males at 4 years). Our results may reflect alterations in the behaviour and life history tactics of elderly males to maintain reproductive fitness in the face of competition from healthier, younger males. Two non-exclusive possibilities suggest themselves: first, elderly males could be showing some form of 'terminal investment' (Clutton-Brock, 1984), in which all available resources are ploughed into the remaining reproductive attempt following the onset of physiological senescence, and second, their greater accrued experience in the rut and knowledge of the habitat could be allowing them to compensate for loss of function. Further analyses of available behavioural and life history data would allow us to test these possibilities and gain a better understanding of how sexual selection and senescence interact in this population.

4.3. Age-related changes in ranging behaviour

The pronounced and sex-dependent ageing patterns in home range size and quality are rare examples of behavioural changes in late life from a wild mammal. Evidence from seabirds suggests that ranging behaviour associated with foraging during reproduction may be altered in older individuals, and this effect may be sex dependent. In grey-headed albatrosses, older males were found to take longer foraging trips during incubation and show lower mass gain over the trip compared to middle-aged males (Catry et al., 2006). One study of wandering albatrosses found striking evidence that incubating older males – but not females – tend to forage in more southerly Antarctic waters and spend longer away from the nest and more time flying between spells on the water (Lecomte et al., 2010). However, no evidence of age-related changes in similar foraging metrics was found in either sex in a different population of the same species (Froy et al., 2015). Evidence for changes in space use in late life in mammals has thus far been limited to a study of the locations of moose carcasses killed by wolves on Isle Royale (Montgomery et al., 2014). This study showed differences in the locations of wolf-killed 'senescent' moose (identified based on degree of osteoarthritis or periodontal disease rather than age) compared to 'non-senescent' animals. Senescent moose were more likely to be found in habitats associated with lower predation risk, suggesting habitat selection changes associated with age-related pathologies (Montgomery et al., 2014). Our finding that female Soay sheep have smaller home ranges as they age could be associated with reduced mobility. Whilst sarcopenia-like changes in muscle structure and osteoarthritis have been detected in wild mammals (Hindle et al., 2009a, 2009b; Peterson et al., 2010; Arthur et al., 2015), we think this an unlikely explanation. Home ranges and foraging routes are rather limited in Soay sheep; certainly compared to the thousands of miles travelled by foraging albatrosses. Furthermore, we would expect to see similar changes in both sexes but instead observe an increase in home range size with age in males. It may be that older females are competitively excluded from some areas of higher quality grazing by younger conspecifics. However, the striking differences between the sexes point to marked sexual differences in behavioural changes in later life. The larger average home range sizes in males are largely due to their behaviour during the rut when they roam widely in search of females, and it seems likely that variation in male behaviour at this time of year drives age-related variation in home range size and quality. On the other hand, female behaviour may be expected to be more consistent throughout the year. Further work that explores seasonal differences in ranging behaviour is clearly warranted to better understand the patterns observed here, and the possibility that age-related changes in adult ranging behaviour and habitat use could underpin sex differences in age-related fitness declines in the wild certainly deserves further investigation.

5. Conclusions

The assumption that mutations, drugs and environmental interventions that extend lifespan will also extend healthspan rests, at least to some degree, on synchrony of senescence among different organs, systems and phenotypic traits. Yet asynchrony of senescence has been documented in humans, laboratory models and wild animals (Walker and Herndon, 2010; Nussey et al., 2013; Bansal et al., 2015). The present study represents the most striking evidence to date of asynchrony of senescence among phenotypic traits from a natural population. Laboratory models offer exquisite insights into effects of single genes, pathways and interventions in a single environment on lifespan and the maintenance of physiological function. However, the use of non-model systems, including those in the wild, offer important and complementary insights: from the identification of novel pathways and mechanisms that might regulate ageing and repair physiological damage (Austad, 2010) to a more general understanding of the cause of variation in ageing within genetically heterogeneous populations of long-lived species experiencing challenging environments (Nussey et al., 2013). Importantly, in the context of questions about the synchrony of senescence, evolutionary theory and studies of wild populations can help explain how and why natural selection under variable environments may couple or uncouple senescence across physiological systems and phenotypes. Studies like the present one are a descriptive first step in this process. Subsequent research determining the genetic basis of asynchrony of senescence, and estimating age-dependent selection on different traits in natural populations should help illuminate the evolutionary origins of asynchrony of senescence.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.exger.2015.08.003.

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References

Arthur, C., Watt, K., Nussey, D.H., Pemberton, J.M., Pilkington, J.G., Herman, J.S., Timmons, Z.L., Clements, D.N., Scott, P.R., 2015. Osteoarthritis of the temporo-mandibular joint in free-living Soay sheep on St Kilda. Vet. J. 203, 120–125.

Austad, S.N., 2010. Methusaleh's zoo: how nature provides us with clues for extending human health span. J. Comp. Pathol. 141, S10–S21.

Bansal, A., Zhu, L.J., Yen, K., Tissenbaum, H.A., 2015. Uncoupling lifespan and healthspan in *Caenorhabditis elegans* longevity mutants. Proc. Natl. Acad. Sci. 112, E277–E286.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2014. Fitting Linear Mixed-effects Models Using lme4 (arXiv preprint arXiv, 1406.5823).

Bérénos, C., Ellis, P.A., Pilkington, J.G., Pemberton, J.M., 2014. Estimating quantitative genetic parameters in wild populations: a comparison of pedigree and genomic approaches. Mol. Ecol. 23, 3434–3451.

Bérénos, C., Ellis, P.A., Pilkington, J.G., Lee, S.H., Gratten, J., Pemberton, J.M., 2015. Heterogeneity of genetic architecture of body size traits in a free-living population. Mol. Ecol. 24, 1810–1830.

Bonduriansky, R., Maklakov, A., Zjitschek, F., Brooks, R., 2008. Sexual selection, sexual conflict and the evolution of ageing and lifespan. Funct. Ecol. 22, 443–453.

Calenge, C., 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197, 516–519.

Catry, P., Phillips, R.A., Phalan, B., Croxall, J.P., 2006. Senescence effects in an extremely long-lived bird: the grey-headed albatross *Thalassarche chrysostoma*. Proc. R. Soc. B Biol. Sci. 273, 1625–1630.

Charmantier, A., Brommer, J.E., Nussey, D.H., 2014. Quantitative genetics of senescence in wild animals. In: Charmantier, A., Garant, D., Kruuk, L.E.B. (Eds.), Quantitative Genetics in the Wild. Oxford University Press, Oxford, pp. 68–83.

Christensen, K., Doblhammer, G., Rau, R., Vaupel, J.W., 2009. Ageing populations: the challenges ahead. Lancet 374, 1196–1208.

Clutton-Brock, T.H., 1984. Reproductive effort and terminal investment in iteroparous animals. Am. Nat. 123, 212–229.

Clutton-Brock, T., Isvaran, K., 2007. Sex differences in ageing in natural populations of vertebrates. Proc. R. Soc. Lond. B Biol. Sci. 274, 3097–3104.

Clutton-Brock, T.H., Pemberton, J.M., 2004. Soay Sheep: Dynamics and Selection in an Island Population. Cambridge University Press, Cambridge.

Colchero, F., Clark, J.S., 2012. Bayesian inference on age-specific survival for censored and truncated data. J. Anim. Ecol. 81, 139–149.

Coltman, D.W., Bancroft, D.R., Robertson, A., Smith, J.A., Clutton-Brock, T.H., Pemberton, J.M., 1999a. Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. Mol. Ecol. 8, 1199–1209.

Coltman, D.W., Smith, J.A., Bancroft, D.R., Pilkington, J., MacColl, A.D.C., Clutton-Brock, T.H., Pemberton, J.M., 1999b. Density-dependent variation in lifetime breeding success and natural and sexual selection in Soay rams. Am. Nat. 154, 730–746.

Craig, B.H., Pilkington, J.G., Pemberton, J.M., 2006. Gastrointestinal nematode species burdens and host mortality in a feral sheep population. Parasitology 133, 485–496.

Craig, B.H., Pilkington, J.G., Kruuk, L.E.B., Pemberton, J.M., 2007. Epidemiology of parasitic protozoan infections in Soay sheep (*Ovis aries* L.) on St. Kilda. Parasitology 134, 9–21.

Craig, B.H., Tempest, L.J., Pilkington, J.G., Pemberton, J.M., 2008. Metazoan–protozoan parasite co-infections and host body weight in St Kilda Soay sheep. Parasitology 135, 433–441.

Elston, D.A., Moss, R., Boulinier, T., Arrowsmith, C., Lambin, X., 2001. Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. Parasitology 122, 563–569.

Evans, S.R., Gustafsson, L., Sheldon, B.C., 2011. Divergent patterns of age-dependence in ornamental and reproductive traits in the collared flycatcher. Evolution 65, 1623–1636.

Falconer, D.S., Mackay, T.F.C., 1996. Introduction to Quantitative Genetics. 4th ed. Prentice Hall, London.

Feulner, P.G., Gratten, J., Kijas, J.W., Visscher, P.M., Pemberton, J.M., Slate, J., 2013. Introgression and the fate of domesticated genes in a wild mammal population. Mol. Ecol. 22, 4210–4221.

Froy, H., Lewis, S., Catry, P., Bishop, C.M., Forster, I.P., Fukuda, A., Higuchi, H., Phalan, B., Xavier, J.C., Nussey, D.H., 2015. Age-related variation in foraging behaviour in the wandering albatross at South Georgia: no evidence for senescence. PLoS One 10, e0116415.

Gulland, F.M.D., Fox, M., 1992. Epidemiology of nematode infections of Soay sheep (*Ovis aries* L) on St-Kilda. Parasitology 105, 481–492.

Hadfield, J.D., Richardson, D.S., Burke, T., 2006. Towards unbiased parentage assignment: combining genetic, behavioural and spatial data in a Bayesian framework. Mol. Ecol. 15, 3715–3730.

Hammers, M., Richardson, D.S., Burke, T., Komdeur, J., 2012. Age-dependent terminal declines in reproductive output in a wild bird. PLoS One 7, e40413.

Hayward, A.D., Wilson, A.J., Pilkington, J.G., Pemberton, J.M., Kruuk, L.E.B., 2009. Ageing in a variable habitat: environmental stress affects senescence in parasite resistance in St Kilda Soay sheep. Proc. R. Soc. Lond. B Biol. Sci. 276, 3477–3485.

Hayward, A.D., Wilson, A.J., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M., Kruuk, L.E.B., 2011. Natural selection on a measure of parasite resistance varies across ages and environmental conditions in a wild mammal. J. Evol. Biol. 24, 1664–1676.

Hayward, A.D., Wilson, A.J., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M., Kruuk, L.E.B., 2013. Reproductive senescence in female Soay sheep: variation across traits and contributions of individual ageing and selective disappearance. Funct. Ecol. 27, 184–195.

Herndon, L.A., Schmeissner, P.J., Dudaronek, J.M., Brown, P.A., Listner, K.M., Sakano, Y., Paupard, M.C., Hall, D.H., Driscoll, M., 2002. Stochastic and genetic factors influence tissue-specific decline in ageing *C. elegans*. Nature 419, 808–814.

Hindle, A.G., Horning, M., Mellish, J.A.E., Lawler, J.M., 2009a. Diving into old age: muscular senescence in a large-bodied, long-lived mammal, the Weddell seal (*Leptonychotes weddellii*). J. Exp. Biol. 212, 790–796.

Hindle, A.G., Lawler, J.M., Campbell, K.L., Horning, M., 2009b. Muscle senescence in short-lived wild mammals, the soricine shrews *Blarina brevicauda* and *Sorex palustris*. J. Exp. Zool. A Ecol. Genet. Physiol. 311A, 358–367.

Jewell, P.A., Milner, C., Boyd, J.M., 1974. Island Survivors: The Ecology of the Soay Sheep of St. Kilda. Athlone Press.

Johnston, S.E., Gratten, J., Berenos, C., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M., Slate, J., 2013. Life history trade-offs at a single locus maintain sexually selected genetic variation. Nature 502, 93–95.

Jones, O.R., Scheuerlein, A., Salguero-Gómez, R., Camarda, C.G., Schaible, R., Casper, B.B., Dahlgren, J.P., Ehrlén, J., García, M.B., Menges, E.S., 2014. Diversity of ageing across the tree of life. Nature 505, 169–173.

Kervinen, M., Lebigre, C., Alatalo, R.V., Siitari, H., Soulsbury, C.D., 2015. Life-history differences in age-dependent expressions of multiple ornaments and behaviors in a lekking bird. Am. Nat. 185, 13–27.

Lande, R., Arnold, S.J., 1983. The measurement of selection on correlated traits. Evolution 37, 1210–1226.

Lecomte, V.J., Sorci, G., Cornet, S., Jaeger, A., Faivre, B., Arnoux, E., Gaillard, M., Trouve, C., Besson, D., Chastel, O., Weimerskirch, H., 2010. Patterns of aging in the long-lived wandering albatross. Proc. Natl. Acad. Sci. U. S. A. 107, 6370–6375.

Lenth, R., Hervé, M., 2014. lsmeans: least-squares means. R Package Version 2.12 (URL: http://CRAN.R-project.org/package=lsmeans).

Martin, J.G., Festa-Bianchet, M., 2011. Age-independent and age-dependent decreases in reproduction of females. Ecol. Lett. 14, 576–581.

Martin, G.M., Bergman, A., Barzilai, N., 2007. Genetic determinants of human health span and life span: progress and new opportunities. PLoS Genet. 3, e125.

Massot, M., Clobert, J., Montes-Poloni, L., Haussy, C., Cubo, J., Meylan, S., 2011. An integrative study of ageing in a wild population of common lizards. Funct. Ecol. 25, 848–858.

Maynard-Smith, J., 1962. Review lectures on senescence. I. The causes of ageing. Proc. R. Soc. Lond. Ser. B Biol. Sci. B157, 115–127.

Milner, J.M., Albon, S.D., Illius, A.W., Pemberton, J.M., Clutton-Brock, T.H., 1999. Repeated selection of morphometric traits in the Soay sheep on St. Kilda. J. Anim. Ecol. 68, 472–488.

Montgomery, R.A., Vucetich, J.A., Roloff, G.J., Bump, J.K., Peterson, R.O., 2014. Where wolves kill moose: the influence of prey life history dynamics on the landscape ecology of predation. PLoS One 9, e91414.

Moorad, J.A., 2014. Individual fitness and phenotypic selection in age-structured populations with constant growth rates. Ecology 95, 1087–1095.

Morrissey, M.B., Parker, D.J., Korsten, P., Pemberton, J.M., Kruuk, L.E.B., Wilson, A.J., 2012. The prediction of adaptive evolution: empirical application of the secondary theorem of selection and comparison to the breeder's equation. Evolution 66, 2399–2410.

Mysterud, A., Yoccoz, N.G., Stenseth, N.C., Langvatn, R., 2001. Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. Proc. R. Soc. Lond. Ser. B Biol. Sci. 268, 911–919.

Nussey, D.H., Coulson, T., Festa-Bianchet, M., Gaillard, J.M., 2008. Measuring senescence in wild animal populations: towards a longitudinal approach. Funct. Ecol. 22, 393–406.

Nussey, D.H., Kruuk, L.E.B., Morris, A., Clements, M.N., Pemberton, J.M., Clutton-Brock, T.H., 2009. Inter- and intra-sexual variation in ageing patterns across reproductive traits in a wild red deer population. Am. Nat. 174, 342–357.

Nussey, D.H., Coulson, T.N., Delorme, D., Clutton-Brock, T.H., Pemberton, J.M., Festa-Bianchet, M., Gaillard, J.M., 2011. Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. Ecology 92, 1936–1947.

Nussey, D.H., Froy, H., Lemaitre, J.-F., Gaillard, J.M., Austad, S.N., 2013. Senescence in natural populations of animals: widespread evidence and its implications for biogerontology. Ageing Res. Rev. 112, 214–225.

Overall, A.D.J., Byrne, K.A., Pilkington, J.G., Pemberton, J.M., 2005. Heterozygosity, inbreeding and neonatal traits in Soay sheep on St. Kilda. Mol. Ecol. 14, 3383–3393.

Packer, C., Tatar, M., Collins, A., 1998. Reproductive cessation in female mammals. Nature 392, 807–811.

Papadopoulos, N.T., Carey, J.R., Katsoyannos, B.I., Kouloussis, N.A., Müller, H.G., Liu, X., 2002. Supine behaviour predicts the time to death in male Mediterranean fruit flies (*Ceratitis capitata*). Proc. R. Soc. Lond. B Biol. Sci. 269, 1633–1637.

Partridge, L., 2010. The new biology of ageing. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 365, 147–154.

Peterson, R.O., Vucetich, J.A., Fenton, G., Drummer, T.D., Larsen, C.S., 2010. Ecology of arthritis. Ecol. Lett. 13, 1124–1128.

Preston, B.T., Stevenson, I.R., Pemberton, J.M., Wilson, K., 2001. Dominant rams lose out by sperm depletion. Nature 409, 681–682.

Preston, B.T., Stevenson, I.R., Lincoln, G.A., Monfort, S.L., Pilkington, J.G., Wilson, K., 2012. Testes size, testosterone production and reproductive behaviour in a natural mammalian mating system. J. Anim. Ecol. 81, 296–305.

Promislow, D.E.L., Fedorka, K.M., Burger, J.M.S., 2006. Evolutionary biology of aging: future directions. In: Masoro, E.J., Austad, S.N. (Eds.), Handbook of the Biology of Aging. Academic Press, Burlington, MA, pp. 217–242.

Rebke, M., Coulson, T., Becker, P.H., Vaupel, J.W., 2010. Reproductive improvement and senescence in a long-lived bird. Proc. Natl. Acad. Sci. U. S. A. 107, 7841–7846.

Regan, C.E., Pilkington, J.G., Pemberton, J.M., Crawley, M.J., 2015w. Vegetation driven spatial variation in lifetime reproductive performance for female, but not male Soay sheep (*Ovis aries*). Ecol. Lett. (in review).
Robinson, M.R., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M., Kruuk, L.E.B., 2006. Live fast, die young: trade-offs between fitness components and sexually antagonistic selection on weaponry in Soay sheep. Evolution 60, 2168–2181.
Tatar, M., Promislow, D.E.I., Khazaeli, A.A., Curtsinger, J.W., 1996. Age-specific patterns of genetic variance in *Drosophila melanogaster*. 2. Fecundity and its genetic covariance with age-specific mortality. Genetics 143, 849–858.
Toigo, C., Gaillard, J.M., Festa-Bianchet, M., Largo, E., Michallet, J., Maillard, D., 2007. Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic. J. Anim. Ecol. 76, 679–686.
van de Pol, M., Verhulst, S., 2006. Age-dependent traits: a new statistical model to separate within- and between-individual effects. Am. Nat. 167, 766–773.
Walker, L.C., Herndon, J.G., 2010. Mosaic aging. Med. Hypotheses 74, 1048–1051.
Ward, E.J., Parsons, K., Holmes, E.E., Balcomb, K.C., Ford, J.K., 2009. The role of menopause and reproductive senescence in a long-lived social mammal. Front. Zoolog. 6.
Williams, G.C., 1957. Pleiotropy, natural selection and the evolution of senescence. Evolution 11, 398–411.
Williams, G.C., 1999. The Tithonus error in modern gerontology. Q. Rev. Biol. 405–415.
Wilson, A.J., Pilkington, J.G., Pemberton, J.M., Coltman, D.W., Overall, A.D.J., Byrne, K.A., Kruuk, L.E.B., 2005. Selection on mothers and offspring: whose phenotype is it and does it matter? Evolution 59, 451–463.

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Accounting for female space sharing in St. Kilda Soay sheep (*Ovis aries*) results in little change in heritability estimates

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Abstract

When estimating heritability in free-living populations, it is common practice to account for common environment effects, because of their potential to generate phenotypic covariance among relatives thereby biasing heritability estimates. In quantitative genetic studies of natural populations, however, philopatry, which results in relatives being clustered in space, is rarely accounted for. The two studies that have been carried out so far suggest absolute declines in heritability estimates of up to 43% when accounting for space sharing by relatives. However, due to methodological limitations these estimates may not be representative. We used data from the St. Kilda Soay sheep population to estimate heritabilities with and without accounting for space sharing for five traits for which there is evidence for additive genetic variance (birthweight, birth date, lamb August weight, and female post-mortem jaw and metacarpal length). We accounted for space sharing by related females by separately incorporating spatial autocorrelation, and a home range similarity matrix. Although these terms accounted for up to 18% of the variance in these traits, heritability estimates were only reduced by up to 7%. Our results suggest that the bias caused by not accounting for space sharing may be lower than previously thought. This suggests that philopatry does not inevitably lead to a large bias if space sharing by relatives is not accounted for. We hope our work stimulates researchers to model shared space when relatives in their study population share space, as doing so will enable us to better understand when bias may be of particular concern.

Introduction

Animal breeders and evolutionary biologists often want to estimate a trait's evolutionary potential. To do this, we estimate genetic components of variance for, and covariance between, traits of interest. In the simplest univariate case, studies typically focus on the additive genetic variance (V_A) and narrow-sense heritability (h^2, the ratio of V_A to phenotypic variance). Through quantitative genetic models, these parameters can be estimated for quantitative traits using data on the phenotypic similarities of individuals of known relatedness (Falconer & Mackay, 1996; Lynch & Walsh, 1998). The development of the 'animal model', a type of mixed effects model, has greatly advanced the application of quantitative genetic analysis to wild populations. This is because the animal model uses information from individuals of varying degrees of relatedness, can cope with missing links in the complex pedigrees so typical of wild populations and is flexible enough to incorporate known or hypothesized nongenetic influences on the phenotype (Wilson *et al.*, 2010). Nongenetic influences on the phenotype can come from a variety of sources. In general, if environmental conditions affect phenotypes, then individuals that share a similar environment will have similar phenotypes but note that there are exceptions: for example, sibling competition can generate greater within-brood variation in growth

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and survival (Nilsson & Svensson, 1996). Environmental effects that are shared by groups of individuals are referred to as 'common environment' effects (Falconer & Mackay, 1996), and these effects generate increased phenotypic similarity. In experimental studies, it is standard practice to break up the association between genes and the local environment by distributing families across, for example cages or tanks. Such an approach is not generally feasible in the wild, and therefore, statistical techniques are used to account for common environment effects (e.g. birth year or habitat type) by including them as fixed or random effects (e.g. McCleery *et al.*, 2004; Vergara *et al.*, 2015). Cross-fostering has however been used to separate out environmentally derived similarity from that due to shared genes in some studies of birds (Hadfield *et al.*, 2006) and mammals (McAdam *et al.*, 2002). A combination of cross-fostering and the animal model is the best way to avoid bias in genetic parameters when common environment effects are strong (Kruuk & Hadfield, 2007); however, cross-fostering is not feasible in all systems used to study quantitative genetics in the wild, for example the ungulates.

Relatives are often clustered in time and/or space and therefore often share environments as well as genes. Where this is the case, common environment effects can be particularly problematic, resulting in biased heritability estimates because we make the mistake of assuming that their similarity is due to shared genes alone (Kruuk & Hadfield, 2007). For example, maternal effects result in offspring born to the same mother being more similar to one another than offspring from different mothers (Falconer & Mackay, 1996). Therefore, failing to account for maternal effects can upwardly bias estimates of V_A and consequently h^2 (Wilson *et al.*, 2005). As a result, it is now routine to account for maternal effects when conducting quantitative genetic analysis. Other sources of common environment effects however have received less attention in quantitative genetic analyses of natural populations. For example, we tend to neglect the fact that relatives can experience similar environments even into adulthood, as a result of natal philopatry (e.g. Rossiter *et al.*, 2002). If this is the case, and the environment is spatially heterogeneous, then we might expect relatives to be more phenotypically similar, because they experience more similar environments. In other words, the value of a trait expressed in an individual may be related to the trait values of individuals at nearby locations, a phenomenon known as spatial autocorrelation (SAC) (Cliff & Ord, 1981; Olalla-Tárraga *et al.*, 2007; Ng *et al.*, 2013). As with maternal effects, failing to account for this type of common environment effect has the potential to bias estimates of V_A and h^2. The potential for SAC to be a source of bias in genetic parameter estimates has been of concern to plant breeders for some time (Cullis & Gleeson, 1989, 1991; Magnussen, 1993; Qiao *et al.*, 2000), particularly in the case of forestry and agricultural variety trials (Dutkowski *et al.*, 2002). Traditionally, experimental design was used to combat this problem, but was often unsuccessful because of the variability in the patterns and scale of spatial variation, resulting from differences in the underlying gradients, ranging from soil and microclimatic effects, to cultural and measurement effects (Dutkowski *et al.*, 2002). Statistical techniques to explicitly model SAC in analyses primarily aimed at estimating genetic parameters have therefore become more popular (Dutkowski *et al.*, 2002). Although the addition of an SAC term generally results in model improvement, the effect of doing so on the genetic variance is variable, with both increases and decreases reported in the plant breeding and forestry literature (Silva *et al.*, 2001; Dutkowski *et al.*, 2002, 2006; Banerjee *et al.*, 2010).

Although studies on plants illustrate that accounting for spatial sources of similarity can be important in deriving accurate heritability estimates, to our knowledge, there have only been two studies that have considered space sharing by relatives beyond the immediate natal environments when conducting quantitative genetic studies on wild animal populations (but see Heckerman *et al.*, 2016 for a recent human study). Firstly, a study of laying date and clutch size in the Wytham wood great tit (*Parus major*) population found that accounting for SAC resulted in an absolute decrease of 25% (from 40% to 15%) in the estimated heritability of laying date, although no such trend was evident for clutch size (Van Der Jeugd & McCleery, 2002). Secondly, a study on the red deer (*Cervus elaphus*) population on the Scottish island of Rum found evidence consistent with space sharing being an important source of bias in heritability estimates (Stopher *et al.*, 2012). In this study, the change in the estimated heritability varied substantially, from an absolute change of 43% (from 44% to <1%) in the case of spring home range size to only around 4% for lifetime breeding success (from 4% to <1%) (Stopher *et al.*, 2012). Although these studies have greatly advanced our understanding of how failure to account for spatial structure in wild populations may bias heritability estimates, there is a need to build on these works, using improved methodologies to understand how heritability estimates are affected when space sharing by relatives is not or cannot be accounted for. Firstly, we need to continue to develop methods to account for space sharing within the animal model, given that heritability estimates derived from outdated techniques, such as parent–offspring regression is less accurate (Kruuk, 2004; Akesson *et al.*, 2008). Of the two studies mentioned above, only the one by Stopher *et al.* (2012) used the animal model approach, while Van Der Jeugd & McCleery (2002) conducted parent–offspring regressions for three groups of individuals whose nestboxes were separated by varying distances. The extension of

this approach to additional traits, populations and species will be necessary before there can be any general conclusions about the effect of accounting for space sharing by relatives on heritability estimates. Secondly, we need to make use of the sophisticated methods available to quantify individual space use, such as utilization distributions (UDs – a relative frequency distribution describing the probability of an individual occurring at a particular location at a specific point in time) (Worton, 1989; Kie *et al.*, 2010). Such techniques are however sensitive to the availability of location data (Seaman *et al.*, 1999; Blundell *et al.*, 2001), and the inclusion of individuals with few observations may have influenced the results of Stopher *et al.* (2012) through the under- or overestimation of space use similarity. Thirdly, trait choice is likely to be important when drawing conclusions about the severity of the bias in heritability estimates as a result of not accounting for the space sharing of relatives. For example, Stopher *et al.* (2012) found large decreases in heritability estimates for two home range size (spring and rut) traits when accounting for the space sharing of related animals, leading them to conclude that heritability estimates can decrease dramatically when space sharing is accounted for. Given that they are spatial metrics, the home range size traits were very likely to have a spatially autocorrelated component. They were therefore useful to demonstrate that similarity in shared space can appear as similarity due to shared genes, providing an example of the potential severity of the bias when failing to account for space sharing by relatives. However, there is to our knowledge little evidence to suggest that such traits have a heritable basis, particularly in mammals where home range size has been shown to vary with a wide variety of factors (van Beest *et al.*, 2011). The results for these traits are therefore unlikely to prove representative of the degree of bias in quantitative genetic parameters. There is a need to build on the study by Stopher *et al.* (2012), examining a wider range of traits, and focusing in particular on those that, based on previous research, are believed to be heritable. Indeed, although it is sensible to account for all suspected common environment effects when aiming to accurately estimate heritability, this may not always be possible given data limitations. Therefore, studies are needed to better establish the likely extent of the bias in traits as a result of not accounting for such common environment effects.

Quantitative genetic analyses of wild populations are continuing to grow in popularity (Kruuk *et al.*, 2008). This means it is essential to expand our understanding of potential biases in heritability estimates due to space sharing by related individuals, making use of the rapidly developing methodologies. The St. Kilda Soay sheep (*Ovis aries*) population is an ideal system for doing this. Firstly, females are philopatric, with relatedness increasing with home range proximity (Coltman *et al.*, 2003). As a result, any phenotypic similarity between related females may be partially due to common environment effects resulting from space sharing. Secondly, there is spatial heterogeneity in the environment. Forage availability and quality varies markedly across the study area (Regan *et al.*, 2015), with the highest quality grazing found in the previously cultivated meadows, and increasing density of low palatability species such as *Calluna vulgaris* as elevation increases (Coulson *et al.*, 1999). Thirdly, because the population has been studied intensively for 30 years, we have sufficient data to quantify individual ranging behaviour and relatedness, making it possible to run animal models which include information on individual space use. Indeed, this population has been the focus of quantitative genetic analysis for many years, providing an ideal platform for expanding on these modelling approaches. Furthermore, in contrast to many other long-term studies of natural populations, a genomic relatedness matrix is available in place of a traditional pedigree. The use of this matrix has been recently shown to give more precise quantitative genetic estimates (Bérénos *et al.*, 2014).

We aimed to understand how accounting for space sharing by related females affected our estimates of V_A or V_{MG} (maternal genetic effects) and h^2_T (the total heritability – accounting for additive and maternal genetic effects) or h^2 (the narrow-sense heritability) for five traits that are, based on previous research, believed to have a heritable basis (birthweight, birth date, lamb August weight, adult jaw length and adult metacarpal length). We predicted that individuals which were similar in their space use would be more similar in their phenotype (or the phenotype of their lambs), and that this would be particularly pronounced for birthweight, birth date and August weight, because these traits are closely tied to resource availability. Consequently, we also expected considerable bias in heritability estimates when space sharing was not accounted for. We provide only the second study to look at the effect of space sharing on estimates of heritability. Using improved methodologies, we show that heritability estimates may be less affected by this source of common environment effect than previously thought.

Materials and methods

Study population and data collection

The data used in this paper come from the Soay sheep population on the island of Hirta in the St. Kilda archipelago, Scotland (57°49°N 08°34°W). This population has been unmanaged since its introduction from the neighbouring island of Soay in 1932 (Clutton-Brock *et al.*, 2004), and Hirta is now home to between 700 and 2300 Soay sheep, depending on variation in mortality between years. Sheep residing in the Village Bay

area of Hirta make up approximately one-third of the total island population and have been intensively studied since 1985 (Clutton-Brock *et al.*, 2004).

The majority of lambs are ear-tagged within the first few days of life, making individuals uniquely identifiable. The mortality status of animals is tracked through regular censuses and mortality checks, with the census data also providing information on individual space use. Each August approximately two-thirds of the Village Bay population are caught, at which time each individual is weighed. Because mortality is tracked closely, we are also able to take post-mortem trait measurements from many animals, including jaw and metacarpal length. We selected three early life traits, birthweight, birth date and lamb August weight (all treated as a trait of the lamb), and two adult traits, female post-mortem jaw length and female post-mortem metacarpal length. These traits were selected because they had previously been the focus of quantitative genetic study, and because of their potential link with resource availability. See Table 1 for heritability estimates for these traits from previous studies. For the adult traits, we incorporated information on the space sharing of all females with post-mortem jaw and metacarpal length measurements. For the early life traits, we used information on the space sharing of their mothers because at the point of measurement lambs have not developed their own home range. There are strong maternal genetic effects in all three early life traits (Wilson *et al.*, 2005; Bérénos *et al.*, 2014), and we were therefore interested in the change in this term when accounting for the space sharing of related mothers. There is no evidence for significant maternal genetic effects for either of the adult traits, and therefore, we did not estimate them in our analyses.

The analyses presented here were based on phenotypic records for individuals born between 1985 and 2012. Lambs were only included if their mother was dead to ensure that we were estimating lifetime space use for all animals. To prevent maternal rejections, we often delay weighing lambs until a few days after birth. As a result of early growth, the weight measurement will vary given the age at which they are caught. Because of this, we restricted our birthweight analyses to individuals caught within 5 days of birth and included capture age (in days) as a fixed effect in all birthweight models. We measured birth date as the number of days from 1 January, and August weight as the weight in kilograms of a lamb when it was caught in August. Jaw and metacarpal length measurements (in millimetres) were taken from bones that were collected and cleaned following mortality checks (see Beraldi *et al.*, 2007 for more details), and in our analysis, we only consider measurements taken from adult females (26 months or older) as skeletal growth is complete at this point [as indicated by an asymptote in the relationship between age and both jaw and metacarpal length (CER, unpublished results)].

Space use

We opted for two methods of accounting for space sharing within the animal model framework used to estimate the genetic parameters, which are broadly comparable to those used in Stopher *et al.* (2012) (differences are described below). The first involves directly accounting for SAC in the response variable, whereas the second involves quantifying home range similarity for pairs of individuals and incorporating this as an additional matrix. We started by extracting spatial information for each individual. We census the 170 hectare Village Bay area 30 times per year, 10 times in each of the three routine trips to the island (April–May, July–August, October–November). During each census, three fixed routes are walked simultaneously, the identity of all individuals seen is noted, and their grid reference is recorded to the nearest 100 m. We extracted lifetime census

Table 1 Published estimates of the narrow-sense heritability (h^2), maternal genetic effect variance (m^2), and total heritability (h^2_T, when reported), for the five traits considered in this study. Hyphens represent cases where the parameter was not reported. Standard errors are provided in parentheses, where available. Note though that the fixed effects included in our models were similar (but not identical) to those included in models in these analyses. Because variance component ratios were calculated using the sum of the variance components as the denominator, reported heritabilities are conditional on fixed effects.

Trait	h^2	m^2	h^2_T	References
Birthweight (lamb)	0.075 (0.045)	0.119 (0.045)	0.135 (0.045)	Wilson *et al.* (2005)
	0.160	0.250	–	Beraldi *et al.* (2007)
	0.069	0.284	–	Wilson *et al.* (2007)
	0.059 (0.017)	0.155 (0.033)	–	Bérénos *et al.* (2014)
Birth date (lamb)	0.055 (0.036)	0.283 (0.051)	0.197 (0.038)	Wilson *et al.* (2005)
	0.070	0.690		Beraldi *et al.* (2007)
August weight (lamb)	0.047	0.017	–	Wilson *et al.* (2007)
	0.104 (0.026)	0.103 (0.032)	–	Bérénos *et al.* (2014)
Jaw length (adult female)	0.390	–	–	Beraldi *et al.* (2007)
	0.594 (0.070)	–	–	Bérénos *et al.* (2014)
Metacarpal length (adult female)	0.450	–	–	Beraldi *et al.* (2007)
	0.556 (0.072)	–	–	Bérénos *et al.* (2014)

observations for all females, excluding any individuals that had fewer than 49 census observations in total. 49 observations is the minimum number needed to give an asymptote in core home range area, thereby providing a reliable estimate of the home range (see Regan *et al.*, 2015 for details). We transformed these observations onto a grid, so that the most south-westerly census observation (NF091980) became (0,0) and each step on the grid represented a distance of 100 m.

We next estimated individual space use. In the case of the SAC model, each individual had to be assigned a single spatial location. We therefore calculated average lifetime locations for each female, ensuring that this was estimated to the nearest 100 m corresponding to the grid described above. From these grid references, we can consider SAC in either the East–West (column) or South–North axis (row) or both simultaneously. To construct the home range similarity matrix necessary for the second method of accounting for space sharing in our animal models, we first estimated home ranges for each female. We estimated home ranges (100% isopleth) using kernel density methods, calculating the smoothing parameter using the *ad hoc* method, within the package adehabitatHR (Calenge, 2006). Because animals were assigned a grid reference to the nearest 100 m during censuses, individuals frequently have numerous observations with identical grid references, and this can cause problems when estimating home ranges using kernel methods (Tufto *et al.*, 1996). We therefore added a random number between −20 and 20 (representing a distance of up to 20 m) to the X and Y coordinates for each record before estimating home ranges (see Moyes, 2007 and Stopher *et al.*, 2012). Powell (2000) suggests using core home ranges as they correspond to the area an animal uses most intensively, but here we were unable to do this because we could not construct a grid for home range estimation that was of a high enough resolution to give similarity metrics that scaled properly (i.e. between zero and one). We continued to consider only individuals with 49 or more observations, as doing so will still provide more reliable home range estimates, and similarity metrics. We then calculated home range overlap/similarity for all possible pairs of these females using Bhattacharyya's affinity (BA) (Bhattacharyya, 1943; Fieberg & Kochanny, 2005) in adehabitatHR (Calenge, 2006). We used BA (see Fieberg & Kochanny, 2005 for a summary of possible metrics) for two reasons. Firstly, because it uses three dimensional utilization distributions (UDs), which describe both where a home range is located in space and the probability of re-sighting an animal at different points within this home range, it better captures how individuals use different parts of their home range (Fieberg & Kochanny, 2005). Thus, this method provides more informative measures of similarity than metrics that consider only the spatial domain of the home ranges (Fieberg & Kochanny, 2005). Secondly, it scales from zero (no overlap) to one (identical UDs), making it comparable to genetic relatedness, which is important when trying to tease apart the contributions of these sources of similarity. This provided us with a matrix containing pairwise similarity metrics for 931 females that could be incorporated into our models (see Fig. 1 for the distribution of BA values). In contrast to Stopher *et al.* (2012), we excluded individuals with insufficient census data in order to avoid potentially over- or underestimating the bias caused by not accounting for space sharing.

Genomic relatedness matrix

When lambs are caught at birth, they are sampled for genotyping. Individuals that are not caught at birth are sampled in August catches, by chemical immobilization (darting, primarily of males during the rut), or post-mortem. Genotypes at 37 037 informative autosomal single nucleotide polymorphism (SNP) markers on the Ovine SNP50 BeadChip (Illumina, for more information see Bérénos *et al.*, 2014) are available for 5805 sheep spanning the period 1985-2012. The genomic elatedness between all pairs of SNP genotyped individuals was estimated in GCTA v1.04, which estimates the proportion of the genome identity-by-state between individuals (see Bérénos *et al.*, 2014 for more details). This genomic relatedness matrix (GRM) was used in our animal models in place of the more traditional pedigree-derived additive relatedness matrix as it provides more accurate estimates of relatedness, leading to improved separation of direct and maternal genetic effects, and more precise estimates of quantitative genetic parameters (Bérénos *et al.*, 2014).

Analyses

All analyses were conducted in R version 3.1.3 (R Development Core Team, 2008). We partitioned the phenotypic variance in each of the traits into genetic and environmental variance components using univariate animal models in ASReml-R (Butler *et al.*, 2007).

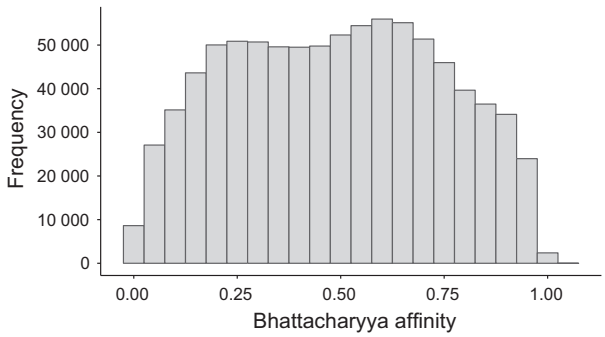

Fig. 1 The distribution of Bhattacharyya affinity/home range overlap values contained in the full **S matrix**.

We included fixed effects to account for variation due to predictable effects such as sex and age. All models for early life traits included sex (two level factor), litter size (two level factor) and maternal age (linear and quadratic terms) as fixed effects. In addition, age at capture in days was included in models of birthweight (as a factor), and lamb August weight (as a covariate). For post-mortem measures, we only included a fixed effect of the age at death in months. After restricting on census observation number and removing individuals lacking the information needed to fit these fixed effects, we had birthweights for 1772 lambs (from 380 females), birth dates for 2124 lambs (404 females), August weights for 1043 lambs (334 females), and 300 and 286 females for jaw and metacarpal length analyses, respectively.

We then added random effects sequentially. Firstly, we included a random effect of individual identity linked with the GRM to estimate the additive genetic effect (V_A, or the additive influence of genes carried by the individual in which the trait was measured). Secondly, we included a random effect of the year of birth, to partition the variance attributable to variation in the environment in the first year of life (V_{YoB}), followed by the identity of the individual's mother in order to estimate maternal effects (assuming that they are entirely environmental) (V_{ME}). Thirdly, in the case of the early life traits, we also fitted a maternal genetic effect (V_{MG}) to decompose the maternal effect variance into maternal permanent environment and maternal genetic components. This is important, as in the case of the early life traits we expect any bias caused by not accounting for space sharing by related females to be found in this maternal genetic effect component. Finally, we estimated the direct-maternal genetic covariance (COV_{am}) to enable the calculation of the total heritability.

We then accounted for space sharing in the following ways. Firstly, to account for spatial dependence in the response variable, we incorporated average lifetime locations by fitting column and row as additional random effects, with an isotropic exponential covariance structure, equivalent to a continuous AR1 times AR1 process (Gilmour *et al.*, 2009). This allows us to account for spatial autocorrelation between the residuals by dividing the residual error variance into spatially dependent and spatially independent residuals. It makes it possible to use an incomplete spatial array (where some intersections are not occupied by an individual) by including column and row as random effects (Dutkowski *et al.*, 2002), while also facilitating the examination of autocorrelation in row and column directions separately (Dutkowski *et al.*, 2002). In models with the SAC process, we estimated both the variance explained by column and row ($V_{column\ and\ row}$), and the strength of the autocorrelation (r). Secondly, we included information on home range similarity by fitting either individual identity (jaw and metacarpal length) or maternal identity (birthweight, birth date and lamb August weight) as an additional random effect, but this time linking it with our spatial similarity matrix (referred to subsequently as the '**S matrix**', with the corresponding variance component referred to as $V_{Smatrix}$).

The total phenotypic variance (denoted as Sum V in Table 2) was estimated as the sum of all variance components, and the variance explained by each of the variance components was calculated as the ratio of the relevant component to the total phenotypic variance. The direct additive-maternal genetic correlation (r_{am}) was calculated as $COV_{am}/\sqrt{V_A.V_{MG}}$. To account for maternal genetic effects and the direct additive-maternal genetic covariance when estimating heritability, we calculated the total heritability (h^2_T) as $(V_A + 1.5COV_{am} + 0.5V_{MG})/SumV$ (sensu Willham, 1972, and following Wilson *et al.*, 2005). We used likelihood ratio tests to assess the significance of random effects, assuming a χ^2 distribution with degrees of freedom equal to the number of additional parameters. However, because variance components cannot be smaller than zero (meaning the boundary condition is violated), the use of one degree of freedom can be overly conservative (Visscher, 2006). To gauge model credibility, we summed the variance component estimates from each model, with large changes in this total variance indicating potential problems with model performance, and that variance component estimates should be interpreted with some caution. In the Results, attention is drawn to models where this was the case, with the interpretation adjusted accordingly. For example code please see Appendix S1.

Results

Early life traits

We found evidence for strong maternal effects on all three early life traits, and models including maternal genetic effects (alongside maternal permanent environment effects and no spatial structure) performed significantly better than those estimating purely environmental maternal effects with no spatial structure (Birthweight – $\chi^2_{(d.f.=1)} = 21.05$, $P < 0.001$; Birth date – $\chi^2_{(d.f.=1)} = 22.82$, $P < 0.001$; August weight – $\chi^2_{(d.f.=1)} = 14.12$, $P < 0.001$). In fact, the estimate of the maternal genetic effect variance was consistently greater than that of the direct heritability for all three early life traits (Table 2). We did not however find any evidence for a significant direct-maternal genetic covariance for any of the three early life traits (Birthweight – $\chi^2_{(d.f.=1)} = 0.001$, $P = 0.97$; Birth date – $\chi^2_{(d.f.=1)} = 0.073$, $P = 0.79$; August weight – $\chi^2_{(d.f.=1)} = 1.90$, $P = 0.17$).

We did however find some differences between these traits in the proportion of variance explained by the spatial term. For birthweight, inclusion of the **S matrix** significantly improved model fit ($\chi^2_{(d.f.=1)} = 13.32$,

Table 2 Variance component estimates and their associated ratios for models including no spatial term, with the **S matrix** (containing home range similarity metrics), or with spatial autocorrelation, for three early life, and two adult traits measured in St. Kilda Soay sheep. Reported are the additive genetic variance (V_A), birth year variance (V_{YoB}), maternal permanent environment variance (V_{ME}), maternal genetic variance (V_{MG}), **S matrix** variance ($V_{Smatrix}$), SAC variance ($V_{column\ and\ row}$), the total variance (Sum V), the autocorrelation coefficient (Autocorrelation (r)), the direct additive-maternal genetic covariance (COV_{am}) and correlation (r_{am}) and the total heritability (h^2_T, accounting for maternal genetic effects and the direct additive-maternal genetic covariance). We provide both the raw variance component/correlation estimates ('Est'), and the proportion of the total variance explained by the term in the case of variance components ('Prop').

	No spatial term		With S matrix		With SAC	
	Est	Prop	Est	Prop	Est	Prop
Birthweight						
V_A	0.003 (0.004)	0.014 (0.018)	0.003 (0.004)	0.014 (0.017)	0.003 (0.004)	0.014 (0.017)
V_{YoB}	0.081 (0.024)	0.336 (0.069)	0.081 (0.025)	0.324 (0.069)	0.081 (0.024)	0.332 (0.070)
V_{ME}	0.007 (0.007)	0.029 (0.030)	0.004 (0.007)	0.018 (0.027)	0.007 (0.007)	0.027 (0.028)
V_{MG}	0.041 (0.011)	0.169 (0.047)	0.038 (0.011)	0.154 (0.043)	0.035 (0.011)	0.146 (0.043)
$V_{Smatrix}$			0.014 (0.010)	0.056 (0.040)		
$V_{Column\ and\ row}$					0.009 (0.010)	0.036 (0.040)
$V_{Residual}$	0.108 (0.005)	0.451 (0.053)	0.108 (0.005)	0.436(0.052)	0.108 (0.005)	0.446 (0.055)
Sum V	0.240		0.249		0.243	
Autocorrelation (r)					0.778 (0.316)	
COV_{am}	$-8.830 \times e^{-4}$ (0.006)		−0.002 (0.005)		$-1.306 \times e^{-3}$ (0.005)	
r_{am}	−0.075 (0.445)		−0.158 (0.427)		−0.119 (0.451)	
h^2_T	0.094 (0.030)		0.080 (0.027)		0.079 (0.028)	
Birth date						
V_A	1.740 (1.077)	0.032 (0.020)	1.759 (1.085)	0.032 (0.020)	1.700 (1.080)	$4.153 \times e^{-5}$ ($2.762 \times e^{-5}$)
V_{YoB}	7.245 (2.208)	0.134 (0.036)	7.282 (2.220)	0.133 (0.036)	7.358 (2.244)	$1.797 \times e^{-4}$ ($5.558 \times e^{-5}$)
V_{ME}	7.478 (2.608)	0.138 (0.049)	8.231 (2.559)	0.150 (0.048)	8.404 (2.588)	$2.053 \times e^{-4}$ ($6.463 \times e^{-5}$)
V_{MG}	13.757 (3.810)	0.255 (0.063)	10.366 (3.503)	0.189 (0.060)	10.887 (3.538)	$2.660 \times e^{-4}$ ($8.781 \times e^{-5}$)
$V_{Smatrix}$			3.314 (2.776)	0.060 (0.048)		
$V_{Column\ and\ row}$					*40 883.58 (1898.87)*	0.999 (0.0001)
$V_{Residual}$	23.793 (1.105)	0.441 (0.035)	23.912 (1.112)	0.436 (0.038)	23.915 (1.111)	$5.842 \times e^{-4}$ ($5.930 \times e^{-8}$)
Sum V	54.014		54.864		40 935.84	
Autocorrelation (r)					1.000 ($2.904 \times e^{-6}$)	
COV_{am}	0.455 (1.539)		0.417 (1.462)		0.185 (1.469)	
r_{am}	0.093 (0.327)		0.098 (0.357)		0.043 (0.348)	
h^2_T	0.171 (0.042)		0.137 (0.041)		$1.813 \times e^{-4}$ ($5.870 \times e^{-5}$)	
August weight						
V_A	0.198 (0.192)	0.036 (0.035)	0.170 (0.189)	0.029 (0.032)	0.163 (0.186)	$1.612 \times e^{-5}$ ($1.921 \times e^{-5}$)
V_{YoB}	2.129 (0.658)	0.391 (0.075)	1.670 (0.527)	0.287 (0.074)	1.970 (0.606)	$1.945 \times e^{-4}$ ($6.178 \times e^{-5}$)
V_{ME}	0.021 (0.191)	0.004 (0.035)	0.043 (0.176)	0.007 (0.030)	0.053 (0.180)	$0.284 \times e^{-6}$ ($1.788 \times e^{-5}$)
V_{MG}	0.737 (0.291)	0.135 (0.052)	0.498 (0.253)	0.086 (0.044)	0.532 (0.260)	$5.255 \times e^{-5}$ ($2.630 \times e^{-5}$)
$V_{Smatrix}$			1.032 (0.629)	0.178 (0.093)		
$V_{Column\ and\ row}$					*10117.65 (765.167)*	*0.999* ($7.399 \times e^{-5}$)
$V_{Residual}$	2.359 (0.182)	0.433 (0.065)	2.397 (0.183)	0.413 (0.064)	2.405 (0.182)	$2.376 \times e^{-4}$ ($1.759 \times e^{-8}$)
Sum V	5.445		5.810		10 122.77	
Autocorrelation (r)					1.000 ($6.989 \times e^{-6}$)	

Table 2 (*Continued*)

	No spatial term		With S matrix		With SAC	
	Est	Prop	Est	Prop	Est	Prop
COV_{am}	0.244 (0.169)		0.222 (0.158)		0.226 (0.157)	
r_{am}	0.638 (0.658)		0.764 (0.871)		0.767 (0.864)	
h^2_T	0.164 (0.046)		0.125 (0.041)		$7.589\times e^{-5}$ ($2.592\times e^{-5}$)	
Jaw length						
V_A	9.974 (2.834)	0.549 (0.129)	9.045 (2.726)	0.480 (0.129)	9.375(2.768)	0.521 (0.131)
V_{YoB}	*4.659*$\times e^{-7}$ (*2.332*$\times e^{-7}$)	*2.562*$\times e^{-8}$ (*1.376*$\times e^{-8}$)	*5.177*$\times e^{-7}$ (*2.324*$\times e^{-8}$)	*2.747*$\times e^{-8}$ (*1.336*$\times e^{-8}$)	$3.327\times e^{-3}$ ($7.729\times e^{-3}$)	$1.848\times e^{-4}$ ($4.305\times e^{-4}$)
V_{ME}	3.603 (1.761)	0.198 (0.092)	3.137 (1.724)	0.166 (0.089)	2.986 (1.752)	0.166 (0.094)
$V_{Smatrix}$			1.548 (1.493)	0.082 (0.074)		
$V_{Column\ and\ row}$					0.546 (0.846)	0.030 (0.046)
$V_{Residual}$	4.604 (2.305)	0.253 (0.136)	5.116 (2.297)	0.271 (0.132)	5.092 (2.330)	0.283 (0.140)
Sum *V*	18.180		18.846		18.003	
Autocorrelation (*r*)					0.630 (0.840)	
Metacarpal length						
V_A	13.400 (2.741)	0.771 (0.110)	13.306 (2.744)	0.761 (0.114)	9.683 (1.498)	0.414 (0.065)
V_{YoB}	*3.008*$\times e^{-7}$ (*3.138*$\times e^{-7}$)	*1.731*$\times e^{-8}$ (*1.878*$\times e^{-8}$)	*1.946*$\times e^{-7}$ (*1.987*$\times e^{-7}$)	*1.113*$\times e^{-8}$ (*1.182*$\times e^{-8}$)	*0.004 (0.374)*	*1.762*$\times e^{-4}$ (*0.016*)
V_{ME}	2.094 (1.402)	0.121 (0.079)	2.054 (1.397)	0.118 (0.078)	2.417 (1.534)	0.103 (0.067)
$V_{Smatrix}$			0.204 (0.683)	0.011 (0.039)		
$V_{Column\ and\ row}$					0.973 (0.842)	0.042 (0.036)
$V_{Residual}$	1.885 (1.966)	0.108 (0.118)	1.923 (1.963)	0.110 (0.117)	10.301 (2.435)	0.441 (0.067)
Sum *V*	17.379		17.479		23.379	
Autocorrelation (*r*)					*2.148*$\times e^{-69}$(NA)	

Standard errors are provided in parentheses, and singular parameters (with 'NA' standard errors)/parameters that were fixed at the boundary are italicized.

$P < 0.001$), and the term explained 5.6% of the variance (Table 2). Its incorporation resulted in small reductions in the estimates of V_{MG} (1.5% (from 16.9% to 15.4%), see Table 2) and V_{ME} (1.1% (from 2.9% to 1.8%), see Table 2) and therefore a negligible reduction in h^2_T (1.4% (from 9.4% to 8.0%), see Table 2). We found a similar trend when using the SAC models, again with a significant improvement in model fit when the spatial terms were added ($\chi^2_{(d.f.=1)} = 10.56$, $P = 0.014$). The autocorrelation parameter indicated positive SAC ($r = 0.80$), but column and row random effects only accounted for 3.6% of the variance and were associated with only a 2.3% reduction (from 16.9 to 14.6%) in the estimate of V_{MG}. The large standard errors, particularly around the estimate of the spatial variance component (Table 2), indicate that the model had some difficulty in estimating them and lends credence to the idea that spatial variation in the environment does not generate substantial variation in lamb birthweight.

Including the **S matrix** also significantly improved model fit in the case of birth date ($\chi^2_{(d.f.=1)} = 9.38$, $P = 0.002$). The spatial term accounted for 6.0% of the variance in birth date, and the change in the estimate of V_{MG} induced by not accounting for space sharing was higher than for birthweight, although still small, declining by 6.6% (from 25.5% to 18.9%) (Table 2, Fig. 2). The reduction in the maternal genetic effect estimate translated into a 3.4% decrease (from 17.1% to 13.7%) in the estimate of h^2_T (Table 2). When it came to the SAC model for birth date, we found evidence for a marginally significant improvement in model fit upon including column and row effects ($\chi^2_{(d.f.=3)} = 7.94$, $P = 0.047$), but there was substantial variance inflation upon incorporation of SAC, with the total variance explained increasing from 54.01 to 40 935.84 (raw observed variance = 48.971). Small changes in the variance explained are not of particular concern, but large changes may indicate that the model has produced poor parameter estimates (Stopher *et al.*, 2012). This was associated with the spatial variance component becoming singular (Table 2), which prevented convergence. This suggests that there is too little spatial variance in the data to enable the estimation of the spatial parameters.

We also found that the **S matrix** significantly improved model fit when added to the model of August weight ($\chi^2_{(d.f.=1)} = 10.12$, $P = 0.001$), but compared with the previous two traits, the spatial term accounted for a much larger proportion of the total variance (17.8%, see Table 2 and Fig. 2). Despite this, the change in h^2_T caused by not accounting for the space sharing of females was on par with birthweight and birth date, with the estimate of V_{MG} reduced by only 4.9% (from 13.5% to 8.6%), and h^2_T reduced by 3.9% (Table 2). The results from the SAC model for August weight were similar to those from the birth date models. The model estimated a very large autocorrelation coefficient of 0.999 (Table 2), indicating very strong positive SAC in lamb August weight. However, the model failed to estimate the spatial variance component, with the estimate for this component increasing in size with each iteration before going singular (Table 2), and therefore preventing convergence. As in the case of birth date, this pattern may indicate that there is too little spatial variance in the data to enable the autocorrelation parameter to be estimated.

Adult traits

As expected from previous analyses, our estimates of h^2 (the ratio of V_A to the total trait variance) were much larger for jaw length and metacarpal length, than for the three early life traits (see Table 2), with only small amounts of variance attributable to birth year and maternal effects (see Table 2 and Fig. 2). We found a marginally significant improvement in model fit when adding the **S matrix** in the case of jaw length ($\chi^2_{(d.f.=1)} = 3.96$, $P = 0.046$), with the term accounting for 8.2% of the variance in the trait (Table 2 and Fig. 2). The incorporation of the **S matrix** did result in a reduction in the estimate of h^2, although this was still relatively small at 6.8% (from 54.9% to 48.0%) (Table 2). For jaw length, the incorporation of SAC did not significantly improve model fit ($\chi^2_{(d.f.=2)} = 1.87$, $P = 0.599$), explaining only 3.0% of the variance and resulting in only a 2.8% decrease (from 54.9% to 52.1%) in the estimate of h^2 (Table 2). In contrast to jaw length, adding the **S matrix** to models of metacarpal length did not improve model fit ($\chi^2_{(d.f.=1)} = 0.11$, $P = 0.74$), and the term accounted for only 1.1% of the variance (Table 2 and Fig. 2). As a result, we saw only a 1% reduction (from 77.1% to 76.1%) in the estimate of h^2 (Table 2). The SAC models echoed this result, as we saw no improvement in model fit upon the inclusion of SAC ($\chi^2_{(d.f.=1)} = -21.81$, $P > 0.99$), with it accounting for only 4.2% of the variance in the trait (Table 2 and Fig. 2). In addition, the very small autocorrelation parameter (that eventually went singular, see Table 2) suggests there is little evidence that animals which are similar in their space use are more similar in their metacarpal lengths than animals which range in very different parts of the study area. Please see Table 3 for fixed effects coefficients for each trait.

Discussion

As predicted, we found that increased similarity in female space use was associated with greater phenotypic similarity. This was most evident for the early life traits, with females that had more similar home ranges having lambs that were more similar in their birthweights, birth dates and August weights. Despite this, and contrary to our expectation, the increase in the

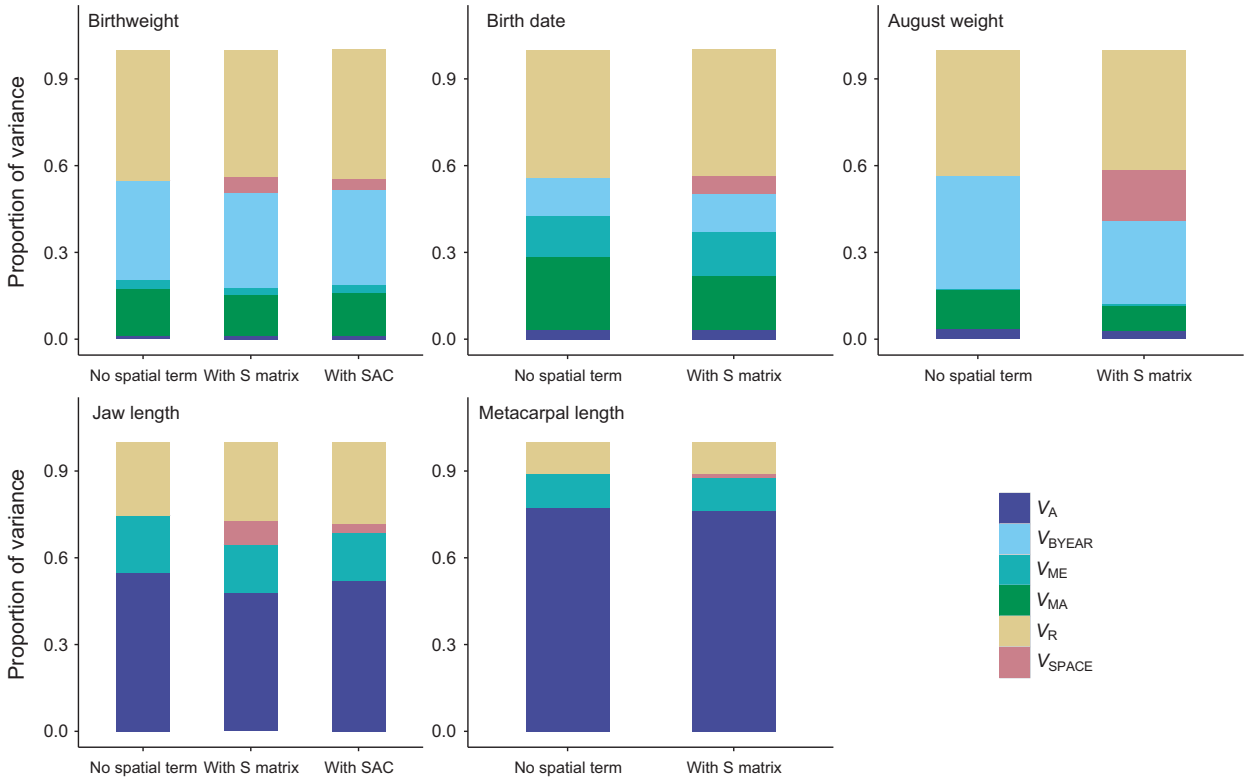

Fig. 2 The proportions of variance explained by different random effects in animal models for three early life, and two adult traits measured in St. Kilda Soay sheep. For all traits, we present the results for models containing no spatial term, and with the home range similarity matrix (or '**S matrix**'), however, we only present the results from spatial autocorrelation models ('With SAC') for the traits where SAC models converged.

(total) heritability estimates caused by not accounting for home range similarity was small, ranging from 1.4% (from 8.0% to 9.4%) to 6.8% (from 48.0% to 54.9%) depending on the trait considered.

Home range similarity generally explained a significant amount of variation in the traits considered, which aligns with previous research on the St. Kilda Soay sheep. Environmental components such as forage availability and quality vary markedly across the study area (Coulson *et al.*, 1999; Regan *et al.*, 2015). Such spatial variation in grazing quality means that sheep inhabiting different regions of the study area have access to food resources of differing quality, something that has been posited to lead to the variation in survival, recruitment and dispersal that we see across hefts (a heft being a group of individuals, regardless of sex or age, that use the same resources in space) (Coulson *et al.*, 1999). Recent work has supported this idea, showing that variation in home range quality (measured as the home range percentage cover of *Holcus lanatus*, a key component of the *Holcus-Agrostis* plant community known to be highly palatable to the sheep (Crawley *et al.*, 2004), is associated with variation in both male and female lifetime reproductive success (Regan *et al.*, 2015). Given the heterogeneity in grazing quality across the study area, and the fact that females exhibit high fidelity to their natal heft (Coltman *et al.*, 2003), it would follow that neighbouring animals are more phenotypically similar, particularly in traits such as birthweight and August weight. This is because these traits are likely to be strongly determined by the quantity and quality of food resources available to the mother during gestation and lactation (Oftedal, 1984). Although the **S matrix** improved model fit for all traits other than metacarpal length, the proportion of variance explained by the spatial term was generally smaller than expected, particularly in the case of birthweight. There is one likely explanation for this result. Hirta's Soay sheep do not conform to the ideal free distribution (Jones 2006). Not only is *Holcus-Agrostis* grassland used by a greater proportion of the population than would be predicted from its availability, but its occupancy actually increases with sheep density (Jones 2006). This likely means that changes in population density compensate to some degree for the variation in grazing quality.

There are two conditions that need to be met for heritability estimates to be biased by disregarding the space use of animals. Firstly, relatives must be clustered in

Table 3 Coefficients and standard errors of fixed effects for each of the five traits featured in this study. For early life traits, values are taken from a model including only the fixed effects shown in the table, and additive genetic, birth year, maternal permanent environment, maternal genetic random effects and a direct-maternal genetic covariance. For the adult skeletal traits, values are taken from a model including only the fixed effects below, and additive genetic, birth year and maternal permanent environment random effects.

Trait	Fixed effect	Level	Coefficient	Standard error
Birthweight	Litter size	Singleton	0.000	NA
	Litter size	Twin	−0.795	0.023
	Sex	Female	0.000	NA
	Sex	Male	0.119	0.017
	Maternal age		0.438	0.014
	Maternal age^2		−0.031	0.001
	Capture age	Day zero	0.000	NA
	Capture age	Day one	0.245	0.042
	Capture age	Day two	0.397	0.041
	Capture age	Day three	0.481	0.044
	Capture age	Day four	0.518	0.049
	Capture age	Day five	0.552	0.057
Birth date	Litter size	Singleton	0.000	NA
	Litter size	Twin	0.003	0.330
	Sex	Female	0.000	NA
	Sex	Male	0.015	0.024
	Maternal age		−0.016	0.190
	Maternal age^2		0.0001	0.016
August weight	Litter size	Singleton	0.000	NA
	Litter size	Twin	−3.441	0.145
	Sex	Female	0.000	NA
	Sex	Male	1.521	0.107
	Maternal age		1.742	0.093
	Maternal age^2		−0.134	0.008
	Capture age		0.066	0.008
Jaw length	Age at death		0.059	0.006
Metacarpal length	Age at death		0.009	0.006

space as it is under this condition that phenotypic similarity due to shared genes may be confounded with similarity due to space sharing. The reason for this potential bias becomes clear when we consider variance partitioning methods. Assuming genetic and environment effects combine additively to determine phenotype, such that:

$$V_P = V_G + V_E$$

It is apparent that such a model is only valid when there is no genotype-environment covariance. To meet this assumption, any sources of correlation (i.e. common environment effects) must be accounted for elsewhere in the model. Social structure and natal philopatry are common in wild vertebrate populations, having been found in birds (Greenwood, 1980), mammals (Greenwood, 1980), reptiles (Sheridan *et al.*, 2010), amphibians (Helfer *et al.*, 2012) and fish (Mourier & Planes, 2013). As a result, the condition that relatives be clustered in space is likely to be satisfied for many natural populations. The degree of bias induced by failing to account for space sharing by relatives may however vary given the degree to which relatives are clustered in space, and the time scale over which the clustering is maintained. Complications may arise when considering migratory species, given that trait variation may be associated with conditions at either the wintering or breeding ground, or even both (Norris *et al.*, 2004; Ockendon *et al.*, 2013).

The second condition required for bias to occur is that the environment must be spatially heterogeneous, as it is this heterogeneity that will mean relatives are more likely to experience similar fine-scale environmental variation, and therefore appear more similar, than nonrelatives. Again, this condition is likely to be satisfied in studies of natural populations, but the spatial scale, and pattern of this environmental heterogeneity is likely to be important, because it will influence the degree of environmental similarity experienced by relatives, compared to nonrelatives. Although not a necessary condition for bias, trait choice should be carefully considered when drawing conclusions about the effect of including space sharing on heritability estimates. Accurately estimating heritability in quantitative genetic studies will necessitate the accounting of potential sources of common environment effects, such as space sharing by relatives. We therefore advocate for space sharing to be included, where the above conditions are met and where possible, into quantitative genetic analyses. However, it may be fruitful to focus on traits that, based on previous research, are believed to be heritable. Given the relatively limited knowledge surrounding the extent of the bias caused by space sharing, it may be most economical to focus on the wide variety of traits for which substantial heritability is apparent in the literature. Furthermore, the degree of bias in heritability estimates as a result of failing to account for space sharing by related animals will be closely related to the degree of heritability in the trait. Despite fulfilling the above conditions and using traits believed to be heritable, we found no evidence of substantial bias in heritability estimates for any of the five traits studied. This suggests that these conditions alone are necessary but not sufficient to generate substantial bias in heritability estimates. Improving our understanding of philopatry in the St. Kilda Soay sheep will enable us to better put our findings into perspective. For example, we do not currently know how the associations between related individuals change over time. It is likely that these associations are not static, given that we know that female ranging behaviour changes with age in Soay sheep (Hayward *et al.*, 2015). Similarly, it may be that dispersal varies across the study area, or between years, because of variation in habitat quality, resource

availability or population density. Indeed, dispersal is known to vary with environmental conditions in a wide range of species (Matthysen, 2005).

Our results suggest that although spatial effects can cause upward bias of heritability estimates, this is not always the case. This conclusion contrasts to those drawn in the two previous studies that have examined the change in heritability estimates when accounting for space sharing in wild populations. In both cases, they suggested that the bias was likely to be considerable, potentially up to 25% and 43%, respectively, (Van Der Jeugd & McCleery, 2002; Stopher *et al.*, 2012). Our estimates are likely to be more robust for the following reasons. Firstly, using the animal model rather than parent–offspring regression (as used in Van Der Jeugd & McCleery, 2002), and a genomic relatedness matrix (GRM) instead of a traditional pedigree, the genetic parameter estimates are likely to be more precise (Kruuk, 2004; Akesson *et al.*, 2008; Bérénos *et al.*, 2014) (although note that animal models were used in Stopher *et al.*, 2012). Secondly, when it came to the **S matrix** approach, we only estimated home ranges, and calculated similarity metrics, for females with at least 49 census observations. Kernel density methods are sensitive to the availability of location data (Seaman *et al.*, 1999; Blundell *et al.*, 2001), and we wanted to ensure that our spatial estimates were not influenced by poor home range estimates for individuals with few data, and assumptions of zero overlap for individuals with no data. It is likely that in other studies spatial data will be more limiting than in our case. The number of observations necessary to accurately estimate home ranges will however vary between systems and with the method in which the spatial data were collected. It will therefore be important to calculate the likely number of observations needed for accurate home range estimation on a case-by-case basis. Where smaller spatial data sets are available, it may be possible to run the analyses with subsets of individuals that vary in their number of observations in order to understand how this influences results. In addition, it may be possible to use tools such as Bayesian kernel density estimators (Zhang *et al.*, 2006) to appropriately account for the uncertainty surrounding home range estimates when deriving overlap metrics. Fourth, and finally, by choosing traits that based on previous research were believed to be heritable we hope our results will provide a useful benchmark for further studies of this kind. As mentioned above, trait choice is likely to be important when drawing conclusions about the expected change in heritability estimates upon accounting for the space sharing of relatives. For example, the large change in the estimated heritability for home range size traits upon including space sharing that was uncovered by Stopher *et al.* (2012) suggested that the bias in heritability estimates is likely to be substantial. These traits are very likely to be spatially variable given their close link with food availability (Tufto *et al.*, 1996; Eide *et al.*, 2004). This made them ideal for illustrating the bias that could be expected under a worse-case scenario but such traits are unlikely to yield representative estimates of the degree of bias in quantitative genetic parameters because there is, to our knowledge, little evidence to suggest that they have a heritable basis, particularly in mammals. This suggestion is supported by the fact that the results from **S matrix** models of birthweight were largely comparable between our study and that of Stopher *et al.* (2012). Both the proportion of variance explained by the spatial term (5.6% in our analysis and 5.9% in Stopher *et al.*, 2012) and the change in the estimate of h^2 when not accounting for shared space (1.4% (from 9.4% to 8.0%) in our analysis, and 2.6% (from 28.2% to 25.6%) in Stopher *et al.*, 2012) were of similar magnitude.

The results from SAC models for birthweight reported here were less similar to those of Stopher *et al.* (2012). In our analysis, the results from the two methods were generally comparable, but in the analysis by Stopher *et al.* (2012), incorporation of the SAC process resulted in the proportion of variance explained by the spatial term increasing to 19.5% (from 5.9% when using the **S matrix**), and an absolute change in the estimate of h^2 of 14.4%. As Stopher *et al.* (2012) suggest, their results may indicate that different spatial processes are at work, but there was some indication that their SAC model could not estimate the autocorrelation coefficient, given that it was fixed at the boundary. Furthermore, the standard error around the variance component estimate for the spatial term was very large (estimate = 0.336, standard error = 0.700), suggesting that there may be little spatial variation in birthweight. Consequently, our results appear to be more closely aligned with those of Stopher *et al.* (2012) than it may at first seem.

In the light of this work, we make some recommendations for future studies aiming to account for space sharing by relatives when running quantitative genetic analyses. In some cases, our SAC models poorly estimated the autocorrelation parameter and the variance explained by SAC. Although these models can indicate whether there is spatial dependence in a trait, it is difficult to put weight on the estimates of the spatial variance component and therefore on the change in the estimated heritability. The problems we and Stopher *et al.* (2012) have identified with the SAC models is perhaps unsurprising, given that they were developed for the analysis of agricultural variety trials (Cullis & Gleeson, 1991). The data from such trials differ considerably to those from long-term studies of animal populations, and this has the potential to influence the suitability of SAC approaches. For example, crop and forestry trials deal with nonmobile organisms that have single spatial locations. We can assign animals single locations, making it possible to run SAC models, but

this may reduce our ability to detect a spatial signal, having averaged over detailed information on individual space use. Furthermore, by averaging over each individual's location data multiple animals often have the same average location (at least over the spatial scale we were able to work at), despite the fact that they do vary in their space use. This too could make it difficult to detect a spatial trend. Finally, we can often record the locations of plants at a much higher precision than that of wild animals. For example, in the case of the Soay sheep, census data are only recorded to the nearest 100 m. Therefore, when it comes to studies of wild animals, there is often a much courser grid over which to run these analyses. This is likely to be one of the key reasons for the poor estimation of the autocorrelation parameter and/or the spatial variance component in our SAC models. As a result, we agree with Stopher *et al.* (2012) in advocating the **S matrix** approach. Not only it is relatively straightforward to fit, but also it is arguably the best available way of including information on space use similarity in animal models. This is because it uses similarity metrics that are based on three dimensional utilization distributions, which tell us not only where a home range is located, but also actually to what degree animals use different parts of this home range (Worton, 1989). One potential limitation of the **S matrix** approach is that, by capturing information on home range overlap/similarity, it can say nothing about individuals that live adjacent to each other but have nonoverlapping utilization distributions according to Bhattacharyya's Affinity. Although it is unlikely that two animals could live at close quarters without overlapping at all in their distributions, it may be inappropriate to leave SAC models behind altogether, because they provide a means to capture this information.

Although our work shows that quantitative geneticists may have confidence in their heritability estimates, there is some way to go before we can make informed predictions about the degree of bias in heritability estimates when we cannot, or do not account for spatially derived similarity. As a result, a key avenue for future research is in understanding whether the degree of bias varies between species, given the huge variation in dispersal patterns in nature. This will make it possible to predict the need for spatial components in quantitative genetic models in the future. It is also important to consider precisely what aspect of the environment is varying spatially when conducting these analyses. In our study, we were generally concerned with capturing the effect of variation in resource availability, with such variation likely to impact traits associated with growth. In other studies, however, the focus may be on spatial variation in predation risk due to variation in substrate colour or vegetation structure, or even spatial variation in the social environment due to differences in, for example, density. This focus will dictate which traits are of most interest, or where bias is of greatest concern.

There are two other exciting avenues for research that we wish to draw attention to. Firstly, although we accounted for phenotypic similarity caused by individuals being born in the same year, the current models lack information regarding temporal variation in the environment after the year of birth and temporal changes in space use itself. Currently, these models treat individuals with a given home range overlap, or neighbouring average lifetime locations, equivalently, whether they were alive at the same time or their lives never overlapped. This assumption of equality regardless of temporal overlap is probably over-simplifying, and penalizing the similarity metric for individuals whose lives did not overlap might result in smaller changes in heritability estimates upon including space sharing. Ranging behaviour itself may vary temporally, and therefore, it may be necessary to consider the temporal scale at which space sharing is quantified more carefully. For example, early life traits may be more dependent on environmental variation at a temporal scale below that of the lifetime, because the body mass/condition of adult females is likely determined at this scale. Indeed, a number of mammalian studies have shown variation in adult body mass/condition in relation to temporal variation in the environment (Clutton-Brock & Albon, 1983; Toïgo *et al.*, 2006). It may therefore be preferable to analyse such traits using an **S matrix** constructed at a more appropriate temporal scale. The suitability of this approach will, however, depend on data availability, as animal models are necessarily data hungry. Secondly, although perhaps unlikely in mammals, traits associated with ranging behaviour may have a genetic basis. Indeed, there have now been a number of quantitative genetic studies focusing on traits associated with ranging behaviour and dispersal (Waser & Thomas Jones, 1989; Hansson *et al.*, 2003; Doligez *et al.*, 2009; Charmantier *et al.*, 2011), the majority of which have focused on birds. If there is a genetic element to space use itself, then it is possible that by accounting for space sharing of related individuals heritabilities may be underestimated (Stopher *et al.*, 2012).

In conclusion, we find that despite significant spatial variation in a variety of heritable traits there were only small changes in heritability estimates when we failed to account for the fact that related female Soay sheep share space because of natal philopatry. This suggests that heritability estimates from prior quantitative genetic studies of this population are likely to be reliable. Although this is reassuring, further research will be needed before we can be confident of the generality of these results. We hope that this work will encourage researchers to include spatial processes in their animal models when their data fulfil the conditions under which we would expect bias in heritability estimates by

not accounting for space sharing. Not only that, we hope that they will publish their results, even when heritability estimates are largely unchanged, so that we can better predict when bias may be of particular concern.

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References

Akesson, M., Bensch, S., Hasselquist, D., Tarka, M. & Hansson, B. 2008. Estimating heritabilities and genetic correlations: comparing the 'animal model' with parent-offspring regression using data from a natural population. *PLoS One* **3**: 1–10.

Banerjee, S., Finley, A.O., Waldmann, P. & Ericsson, T. 2010. Hierarchical spatial process models for multiple traits in large genetic trials. *J. Am. Stat. Assoc.* **105**: 506–521.

van Beest, F.M., Rivrud, I.M., Loe, L.E., Milner, J.M. & Mysterud, A. 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *J. Anim. Ecol.* **80**: 771–785.

Beraldi, D., McRae, A.F., Gratten, J., Slate, J., Visscher, P.M. & Pemberton, J.M. 2007. Mapping quantitative trait loci underlying fitness-related traits in a free-living sheep population. *Evolution* **61**: 1403–1416.

Bérénos, C., Ellis, P.A., Pilkington, J.G. & Pemberton, J.M. 2014. Estimating quantitative genetic parameters in wild populations: a comparison of pedigree and genomic approaches. *Mol. Ecol.* **23**: 3434–3451.

Bhattacharyya, A. 1943. On a measure of divergence between two statistical populations defined by their probability distributions. *Bull. Cal. Math. Soc.* **35**: 99–109.

Blundell, G.M., Maier, J.A.K. & Debevec, E.M. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecol. Monogr.* **71**: 469–489.

Butler, D.G., Cullis, B.R., Gilmour, A.R. & Gogel, B.J. 2007. *Analysis of Mixed Models for S Language Environments: ASReml-R Reference Manual, Release 2*. Queensland Department of Primary Industries and Fisheries, Brisbane.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Modell.* **197**: 516–519.

Charmantier, A., Buoro, M., Gimenez, O. & Weimerskirch, H. 2011. Heritability of short-scale natal dispersal in a large-scale foraging bird, the wandering albatross. *J. Evol. Biol.* **24**: 1487–1496.

Cliff, A. & Ord, J. 1981. *Spatial Processes: Models and Applications*. Pion, London.

Clutton-Brock, T.H. & Albon, S.D. 1983. Climatic variation and body weight of red deer. *J. Wildl. Manage.* **47**: 1197–1201.

Clutton-Brock, T.H., Pemberton, J.M., Coulson, T., Stevenson, I.R. & Maccoll, A.D.C. 2004. Individuals and populations. In: *Soay Sheep: Dynamics and Selection in an Island Population* (T.H. Clutton-Brock & J.M. Pemberton, eds), pp. 1–13. Cambridge University Press, Cambridge.

Coltman, D.W., Pilkington, J.G. & Pemberton, J.M. 2003. Fine-scale genetic structure in a free-living ungulate population. *Mol. Ecol.* **12**: 733–742.

Coulson, T., Albon, S., Pilkington, J. & Clutton-Brock, T. 1999. Small-scale spatial dynamics in a fluctuating ungulate population. *J. Anim. Ecol.* **68**: 658–671.

Crawley, M.J., Albon, S.D., Bazely, D.R., Milner, J.M., Pilkington, J.G. & Tuke, A.L. 2004. Vegetation and sheep population dynamics. In: *Soay Sheep: Dynamics and Selection in an Island Population* (T.H. Clutton- Brock & J.M. Pemberton, eds), pp. 89–111. Cambridge University Press, Cambridge.

Cullis, B.R. & Gleeson, A.C. 1989. Efficiency of neighbour analysis for replicated variety trials in Australia. *J. Agric. Sci.* **113**, 233–239.

Cullis, B.R. & Gleeson, A.C. 1991. Spatial analysis of field experiments-an extension to two dimensions. *Biometrics* **47**: 1449–1460.

Doligez, B., Gustafsson, L. & Pärt, T. 2009. 'Heritability' of dispersal propensity in a patchy population. *Proc. Biol. Sci.* **276**: 2829–2836.

Dutkowski, G.W., Silva, J.C.E., Gilmour, A.R. & Lopez, G.A. 2002. Spatial analysis methods for forest genetic trials. *Can. J. For. Res.* **32**: 2201–2214.

Dutkowski, G.W., Costa e Silva, J., Gilmour, A.R., Wellendorf, H. & Aguiar, A. 2006. Spatial analysis enhances modelling of a wide variety of traits in forest genetic trials. *Can. J. For. Res.* **36**: 1851–1870.

Eide, N., Jepsen, J. & Prestrud, P. 2004. Spatial organization of reproductive Arctic foxes Alopex lagopus: responses to changes in spatial and temporal availability of prey. *J. Anim. Ecol.* **73**: 1056–1068.

Falconer, D. & Mackay, T.F. 1996. *Introduction to Quantitative Genetics*, 4th Edn. Prentice Hall, London.

Fieberg, J. & Kochanny, C. 2005. Quantifying home-range overlap: the importance of the utilization distribution. *J. Wildl. Manage.* **69**: 1346–1359.

Gilmour, A.R., Gogel, B., Cullis, B.R. & Thompson, R. 2009. *Asreml User Guide Release 3.0*. VSN International Ltd, Hemel Hempstead, UK.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**: 1140–1162.

Hadfield, J.D., Burgess, M.D., Lord, A., Phillimore, A.B., Clegg, S.M. & Owens, I.P.F. 2006. Direct versus indirect sexual selection: genetic basis of colour, size and recruitment in a wild bird. *Proc. Biol. Sci.* **273**: 1347–1353.

Hansson, B., Bensch, S. & Hasselquist, D. 2003. Heritability of dispersal in the great reed warbler. *Ecol. Lett.* **6**: 290–294.

Hayward, A.D., Moorad, J., Regan, C.E., Berenos, C., Pilkington, J.G., Pemberton, J.M. & Nussey, D.H. 2015. Asynchrony

of senescence among phenotypic traits in a wild mammal population. *Exp. Gerontol.* **71**: 56–68.

Heckerman, D., Gurdasani, D., Kadie, C., Pomilla, C., Carstensen, T., Martin, H., Ekoru, K., Nsubuga, R.N., Ssenyomo, G., Kamali, A., Kaleebu, P., Widmer, C. & Sandhu, M.S. 2016. Linear mixed model for heritability estimation that explicitly addresses environmental variation. *Proc. Natl. Acad. Sci. USA* **113**: 7377–7382.

Helfer, V., Broquet, T. & Fumagalli, L. 2012. Sex-specific estimates of dispersal show female philopatry and male dispersal in a promiscuous amphibian, the alpine salamander (Salamandra atra). *Mol. Ecol.* **21**: 4706–4720.

Jones, O.R., Pilkington, J.G. & Crawley, M.J. 2006. Distribution of a naturally fluctuating ungulate population among heterogeneous plant communities: ideal and free? *J. Anim. Ecol.* **75**: 1387–1392.

Kie, J.G., Matthiopoulos, J., Fieberg, J., Powell, R.A., Cagnacci, F., Mitchell, M.S., Gaillard, J.M. & Moorcroft, P.R. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philos Trans. R. Soc. Lond. B. Biol. Sci.* **365**: 2221–2231.

Kruuk, L.E.B. 2004. Estimating genetic parameters in natural populations using the "animal model". *Philos Trans. R. Soc. Lond. B. Biol. Sci.* **359**: 873–890.

Kruuk, L.E.B. & Hadfield, J.D. 2007. How to separate genetic and environmental causes of similarity between relatives. *J. Evol. Biol.* **20**: 1890–1903.

Kruuk, L.E., Slate, J. & Wilson, A.J. 2008. New answers for old questions: the evolutionary quantitative genetics of wild animal populations. *Annu. Rev. Ecol. Evol. Syst.* **39**: 525–548.

Lynch, M. & Walsh, B. 1998. *Genetics and Analysis of Quantitative Traits*. Sinauer, Sunderland.

Magnussen, S. 1993. Bias in genetic variance estimates due to spatial autocorrelation. *Theor. Appl. Genet.* **86**: 349–355.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. *Ecography* **28**: 403–416.

McAdam, A.G., Boutin, S., Réale, D. & Berteaux, D. 2002. Maternal effects and the potential for evolution in a natural population of animals. *Evolution* **56**: 846–851.

McCleery, R., Pettifor, R., Armbruster, P., Meyer, K., Sheldon, B. & Perrins, C. 2004. Components of variance underlying fitness in a natural population of the great tit parus major. *Am. Nat.* **164**: E62–E72.

Mourier, J. & Planes, S. 2013. Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia. *Mol. Ecol.* **22**: 201–214.

Moyes, K. 2007. Demographic consequences of individual variation. PhD thesis, University of Kent, Canterbury, UK.

Ng, J., Landeen, E.L., Logsdon, R.M. & Glor, R.E. 2013. Correlation between Anolis lizard deqlap phenotype and environmentl variation indicates adaptive divergence of a signal important to sexual selection and species recognition. *Evolution* **67**: 573–582.

Nilsson, J. & Svensson, M. 1996. Sibling competition affects nestling growth strategies in marsh tits. *J. Anim. Ecol.* **65**: 825–836.

Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.W. & Ratcliffe, L.M. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proc. Biol. Sci.* **271**: 59–64.

Ockendon, N., Leech, D. & Pearce-Higgins, J.W. 2013. Climatic effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carry-over effects from wintering grounds. *Biol. Lett.* **9**: 1–4.

Oftedal, O.T. 1984. Body size and reproductive strategy as correlates of milk energy output in lactating mammals. *Acta Zool. Fenn.* **171**: 183–186.

Olalla-Tárraga, M.Á., Rodríguez, M.Á. & Ángel, M. 2007. Energy and interspecific body size patterns of amphibian faunas in Europe and North America: anurans follow Bergmann's rule, urodeles its converse. *Glob. Ecol. Biogeogr.* **16**: 606–617.

Powell, R. 2000. *Animal Home Ranges and Territories and Home Range Estimators*. Columbia University Press, New York, NY. pp. 65–110.

Qiao, C.G., Basford, K.E., DeLacy, I.H. & Cooper, M. 2000. Evaluation of experimental designs and spatial analyses in wheat breeding trials. *Theor. Appl. Genet.* **100**: 9–16.

R Development Core Team. 2008. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Regan, C.E., Pilkington, J.G., Pemberton, J.M. & Crawley, M.J. 2015. Sex differences in relationships between habitat use and reproductive performance in Soay sheep (*Ovis aries*). *Ecol. Lett.* **19**: 171–179.

Rossiter, S.J., Jones, G., Ransome, R.D. & Barratt, E.M. 2002. Relatedness structure and kin-biased foraging in the greater horseshoe bat (*Rhinolophus ferrumequinum*). *Behav. Ecol. Sociobiol.* **51**: 510–518.

Seaman, D., Millspaugh, J., Kernohan, B., Brundige, G., Raedeke, K. & Gitzen, R. 1999. Effects of sample size on kernel home range estimates. *J. Wildl. Manag.* **63**: 739–747.

Sheridan, C.M., Spotila, J.R., Bien, W.F. & Avery, H.W. 2010. Sex-biased dispersal and natal philopatry in the diamondback terrapin, Malaclemys terrapin. *Mol. Ecol.* **19**: 5497–5510.

Silva, J.C.E., Dutkowski, G.W. & Gilmour, A.R. 2001. Analysis of early tree height in forest genetic trials is enhanced by including a spatially correlated residual. *Can. J. For. Res.* **31**: 1887–1893.

Stopher, K.V., Walling, C.A., Morris, A., Guinness, F.E., Clutton-Brock, T.H., Pemberton, J.M. & Nussey, D.H. 2012. Shared spatial effects on quantitative genetic parameters: accounting for spatial autocorrelation and home range overlap reduces estimates of heritability in wild red deer. *Evolution* **66**: 2411–2426.

Toïgo, C., Gaillard, J.M., Van Laere, G., Hewison, M. & Morellet, N. 2006. How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. *Ecography* **29**: 301–308.

Tufto, J., Andersen, R. & Linnell, J. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *J. Anim. Ecol.* **65**: 715–724.

Van Der Jeugd, H.P. & McCleery, R. 2002. Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. *J. Evol. Biol.* **15**: 380–387.

Vergara, P., Fargallo, J.A. & Martínez-Padilla, J. 2015. Genetic basis and fitness correlates of dynamic carotenoid-based ornamental coloration in male and female common kestrels *Falco tinnunculus*. *J. Evol. Biol.* **28**: 146–154.

Visscher, P.M. 2006. A note on the asymptotic distribution of likelihood ratio tests to test variance components. *Twin Res. Hum. Genet.* **9**: 490–495.

Waser, P.M. & Thomas Jones, W. 1989. Heritability of dispersal in banner-tailed kangaroo rats, *Dipodomys spectabilis*. *Anim. Behav.* **37**: 987–991.

Willham, R.L. 1972. The role of maternal effects in animal breeding. 3. Biometrical aspects of maternal effects in animals. *J. Anim. Sci.* **35**: 1288–1293.

Wilson, A.J., Coltman, D.W., Pemberton, J.M., Overall, A.D.J., Byrne, K.A. & Kruuk, L.E.B. 2005. Maternal genetic effects set the potential for evolution in a free-living vertebrate population. *J. Evol. Biol.* **18**: 405–414.

Wilson, A.J., Pemberton, J.M., Pilkington, J.G., Clutton-Brock, T.H., Coltman, D.W. & Kruuk, L.E.B. 2007. Quantitative genetics of growth and cryptic evolution of body size in an island population. *Evol. Ecol.* **21**: 337–356.

Wilson, A.J., Réale, D., Clements, M.N., Morrissey, M.M., Postma, E., Walling, C.A., Kruuk, L.E.B. & Nussey, D.H. 2010. An ecologist's guide to the animal model. *J. Anim. Ecol.* **7**: 13–26.

Worton, B. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**: 164–168.

Zhang, X., King, M.L. & Hyndman, R.J. 2006. A Bayesian approach to bandwidth selection for multivariate kernel density estimation. *Comput. Stat. Data Anal.* **50**: 3009–3031.

Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article: **Appendix S1** Example R code for the analysis of birth weight.

Data deposited at Dryad: doi: 10.5061/dryad.qv145

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Original Article

Female Soay sheep do not adjust their maternal care behaviour to the quality of their home range

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Resource availability, through its impact on the costs and benefits of parental care, is expected to influence parental care behaviour. There has, to our knowledge, been no attempt to understand how variation in the resource use of wild individuals influences individual parental care behaviour. To understand how natural resource variability affects maternal care in female St. Kilda Soay sheep, we selected 69 females whose home ranges varied in quality (measured as the mean percentage cover of *Holcus lanatus*), and recorded the behaviour of each individual and her lamb over the period of maternal care. Home range quality did not influence suckling or non-suckling behaviours of the female or her lamb, suggesting that maternal care did not vary with a female's access to resources. Growth rate analyses confirmed the behavioural results, with no association between home range quality and the weight gain of lambs between birth and weaning. This work suggests that female Soay sheep faced with poorer resources do not favour their own future success over that of their lamb, and thereby do not exhibit a conservative reproductive strategy. This may be because when resource levels are high during the summer, females are able to offset the costs of lactation by consuming additional resources, regardless of the location of their home range. Our results suggest that more studies characterizing the environment experienced by individual animals will be necessary to fully understand how individuals alter their behaviour in response to temporal and spatial variation in the environment.

Key words: **home range quality, maternal care, resource availability, Soay sheep, ungulate, wild.**

INTRODUCTION

Parents of many species provide their offspring with parental care, which can be defined as any parental trait that increases the fitness of the offspring, and that originated for or is currently maintained for this purpose (Smiseth et al. 2012). Providing care often comes at a cost to the parent's own survival and future reproduction, at which point it can be termed parental investment (Smiseth et al. 2012). To maximize their own lifetime reproductive success, parents must balance the benefits of investing in current offspring against the costs of reduced future reproductive opportunities. As a result, parents are expected to adjust the level of care they provide to the benefits of care to their offspring and the cost to themselves (Winkler 1987). Many factors have the potential to influence the relative costs and benefits of parental care thereby contributing to variation in the level of parental care. These factors can relate to the offspring themselves, for example their relatedness to the parent (Møller and Birkhead 1993; Dixon et al. 1994) or their sex (Hasselquist and Kempenaers 2002). Similarly, in species where care is shared among multiple individuals, the benefit can vary depending on the amount of care provided by the focal parent as well the amount provided by its partner (Lessells 2012) or any helpers (MacColl and Hatchwell 2003). The environmental conditions that a parent experiences can also alter the benefits of care to offspring and/or the costs of providing care to the parent, and thereby influence the level of parental care provided (Clutton-Brock 1991).

The environment an individual experiences is complex, composed of a wide variety of biotic and abiotic factors. Research has shown that parental care behaviours are influenced by an array of environmental components, from predation risk (Fontaine and Martin 2006; Huang and Wang 2009) and the social environment (Bales et al. 2002; Russell et al. 2008; Brouwer et al. 2014) to weather conditions (Thierry et al. 2013; Öberg et al. 2015) and resource availability (Scornavacca et al. 2016). Much of the literature on the effects of environmental variation has focused on resource availability, which is unsurprising given that resource

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availability dictates the amount of energy that is available for growth, survival, or reproduction. However, empirical work is yet to uncover a consistent relationship between resource variability and parental care. Many studies report no influence of resource availability on parental care decisions (e.g. Whittingham and Robertson 1994, Andrews et al. 2017), whilst other studies find reductions (e.g. Whittingham and Robertson 1994), or increases in parental care with increased resource availability (e.g. Rachlow and Bowyer 1994; Wong and Kölliker 2012; Markman et al. 2002). The diversity evident in the existing literature may derive from differences in the effect of resource variation on the survival and reproductive value of adults versus offspring (Clutton-Brock 1991). Decreased resource availability is expected to result in increased parental care if the parent's potential for reproduction in the future is low relative to that of the offspring (Clutton-Brock 1991). However, if future reproduction of the parent is less affected by resource scarcity than the future reproduction of the offspring, then a decrease in resource availability should be associated with reductions in care because parents should favour their own future reproduction (Clutton-Brock 1991). This argument suggests that the effect of resource variation on parental care is linked closely with life history. For example, females of long-lived iteroparous species, such as ungulates, might adopt a conservative reproductive strategy, such that when faced with resource scarcity they allocate fewer resources to their offspring and maintain their own condition (Martin and Festa-Bianchet 2010). This is because their fitness is more dependent on their own survival than their reproductive success in any single year (Gaillard and Yoccoz 2003).

Despite the long-established interest in the effect of resource availability on parental care, there are still substantial gaps in our understanding. First, much of the previous research has utilized bird systems. Most birds have bi-parental care (Clutton-Brock 1991), which is a rare pattern of care in most other taxa, including mammals. In most non-avian taxa, a single parent (usually the female) provides all care to the offspring (Stahlschmidt 2011). Where both parents provision the offspring, the response of one parent to environmental conditions may be conditional on the behaviour of the other parent (Lessells 2012), which could make it difficult to detect an association between environmental conditions and parental care. Second, supplementation experiments are commonly used to understand how resource availability affects parental care. Such experiments might come at a cost in terms of loss of biological realism and therefore it may be beneficial to complement the use of experimental manipulations with studies using natural variation in resources. Third, the limited number of studies on naturally occurring variation in resources in wild populations are often based on comparisons between different populations (e.g. Tremblay et al. 2004). This practice is problematic because it is difficult to separate the effects of environmental conditions from behavioural differences between populations due to genetic differentiation (Johannesson and Johannesson 1996). Fourth, care must be taken to quantify environmental conditions in a way that accurately reflects its impact on the study organism. Much of the literature has focused on the effect of between-year variation in resource availability on parental investment, using population density and/or mortality as a proxy for resource availability (e.g. Robertson et al. 1992). This approach does not account for the fact that individuals are more likely to respond to the resource levels they experience in their home range than to the resources available to the population as a whole. Movement ecologists have developed sophisticated methods to estimate individual space use (e.g. kernel density home range estimators), making it possible to examine the effects of fine-scale resource variation on individual parental care decisions. However, to our knowledge, these approaches have not been used to study the effect of resource variation on parental care. Finally, studies tend not to record the behaviour of the offspring. However, any influence of environmental conditions on offspring behaviour may influence the parent's behaviour, thereby potentially influencing any relationship between parental behaviour and environmental variation such as resource availability.

The St. Kilda population of Soay sheep is an ideal system in which to study the effect of resource variation on parental care behaviour. The long term data available (Clutton-Brock et al. 2004) make it possible to quantify both between-individual and between-year variation in environmental conditions. Furthermore, individuals are marked with unique ear tags, making it possible to record the behaviours of specific females and their lambs. Body weight is associated with many aspects of female reproduction and survival in Soay sheep, influencing the probability of conception in the first year, the likelihood that females bear twins, and the probability of over-winter survival (Clutton-Brock et al. 2004). A female's body weight is also closely tied to the birth weight of her lambs (Clutton-Brock et al. 2004), which in turn affects their early survival (Jones et al. 2005). Body weight and condition are likely to be closely related to home range quality, and there is marked variation in forage quality and quantity across the study area (Coulson et al. 1999; Regan et al. 2016). *Holcus-Agrostis* (HA) grassland is the most productive plant community on the island (as determined using grazing exclosures), containing the highest live standing-crop biomass (Crawley et al. 2004). This community is also highly palatable to the sheep, with sheep selecting for this community even at high density (Jones et al. 2006). The aim of this study is to understand how natural variation in resource availability affects patterns of maternal care in female St. Kilda Soay sheep (*Ovis aries*). To this end, we studied the parental behaviour of females and the sucking behaviour of their lambs over the period of maternal care in 2014 and 2015. We selected females based on the quality of their home range, measured as the mean percentage cover of *Holcus lanatus* (one of the dominant species in *Holcus-Agrostis* grassland) within their core home range, before following them in the field after the birth of their lambs in April/May until weaning in August.

METHODS

Study population

Soay sheep were introduced to the island of Hirta in 1932 from the neighbouring island of Soay in the St. Kilda archipelago, Scotland (57°49° N 08°34° W). Since their introduction they have been entirely unmanaged, and the total island population now ranges from 700 to 2300 individuals, depending on variation in mortality between years. Hirta's sheep have been studied since the early 1960s, but intensive study of the Village Bay population (containing ~30% of the total island population) commenced in 1985. To enable identification individual sheep are marked with plastic ear tags shortly after birth and within the Village Bay area more than 95% of animals are tagged (Clutton-Brock et al. 2004). A combination of mortality checks and censuses enable the monitoring of individual survival, whilst also providing information on individual space use. Female Soay sheep are philopatric, with more than 80% remaining in their natal heft throughout their life (Coltman et al. 2003). Given the home range fidelity exhibited by female Soay

sheep and the substantial spatial heterogeneity in grazing quality across the study area, individuals vary in their access to resources (Regan et al. 2016) and consequently will likely vary in their reproductive investment decisions.

Home range estimation and animal selection

Researchers from the Soay sheep project travel to St. Kilda three times per year (April-May, July-August, October-November), and conduct ten censuses of the Village Bay area during each trip. During each census, three fixed routes are walked simultaneously and the identity and grid reference (to the nearest 100 meters) of all encountered individuals is noted. In the Spring of 2014 and 2015, we extracted census observations for all females that were recorded as being alive in the preceding census, were aged between 3 and 8 years (to exclude young and geriatric individuals due to likely differences in their behaviour), and that had at least 49 census observations in total. This is because 49 observations is the minimum number needed to reach an asymptote in core home range area when estimating lifetime home ranges, indicating that the core home range has been reliably estimated (see Regan et al. 2016 for details). We transformed these observations onto a grid, so that the most south-westerly census observation (NF091980) became (0,0) and each step on the grid represented a distance of 100 meters. Because the census procedure means that animals are assigned a grid reference to the nearest 100 meters, individuals frequently have numerous observations with identical grid references. This can cause problems when estimating home ranges using kernel methods (Tufto et al. 1996) and we therefore added a random number between −20 and 20 (representing a distance of up to 20 meters) to both the X and Y coordinates of each observation before home range estimation (see Moyes 2007; Stopher et al. 2012).

Home ranges were calculated using census observations from all years of a female's life prior to the observation period to maximize the number of potential study animals, and also because data were not yet available at the time of animal selection for all censuses in the year preceding observation (we have since conducted analyses using annual home range estimates/resource selection functions—see below for details). We estimated core home ranges (70% isopleth; see Regan et al. 2016 for details) using kernel density methods with the package "adehabitatHR" (Calenge 2006) in R version 3.1.3 (R Development Core Team 2008). Use of the reference bandwidth (h_{ref}) can result in over-smoothing and consequently biased home range estimates, leading Kie (2013) to suggest a rule-based "ad hoc" method for estimating the bandwidth. This method involves sequentially reducing h_{ref} until the 95% kernel home range polygon fragments or lacuna appear, at which point the process is stopped (Kie 2013). We estimated home ranges using both methods, finding that in many cases the home range was already fragmented when using h_{ref}, preventing any further reduction in the smoothing parameter, and that the use of the "ad hoc" bandwidth, where possible, had very little impact on estimates of the percentage cover of *H. lanatus*, and therefore did not change our results. As a result, we present analyses using home ranges calculated using h_{ref}. Though data from both 2014 and 2015 field seasons could be used for the analyses described below, it must be noted that, in 2014, females were selected specifically based on their access to resources (see below), whereas in 2015 their home ranges were calculated to enable us to account for space use when selecting females based on the predicted growth of their lambs.

We quantified the variation in home range quality by characterizing the vegetation present within each individual's home range. Using the Ordnance Survey Grid, the Village Bay study area is divided into 160 one hectare squares (100 × 100 m) [the remaining 10 hectares were not surveyed for vegetation due to access difficulties and/or a lack of vegetation (some are covered by scree)]. Between 2008 and 2012 complete species lists were compiled for the vascular plants in each hectare, and the percentage cover of each species (to the nearest 5%) was scored by eye. MJC collected all botanical data so there were no between-observer sources of error. Ocular cover estimation is the only practical method for hectare-sized plots because it averages over the within-plot spatial heterogeneity. Furthermore, calibrations of visual cover estimates against biomass data in related studies have shown that the results from the two methods are strongly correlated (e.g. Allan and Crawley 2011, MJC, unpublished analysis). Plant community boundaries are the same as described in Gwynne et al. (1974), and there has been no detectable change in the botanical composition of these communities since detailed botanical recording began in 1993 (MJC, unpublished results). We obtained home range quality metrics by calculating the percentage cover of *H. lanatus* in individual core home ranges. We did this by taking a weighted mean of the percentage covers recorded in the hectares contained within each individual's home range. The proportion of the hectare contained within the home range was used as a weight to ensure that the varying contributions of constituent hectares was taken into account.

Upon completion of both field seasons, we estimated home range quality metrics and individual resource selection functions for the year preceding behavioural observation. We focused on the year preceding observation for two reasons. First, it was not possible to assess individual space use for the precise period in which behavioural observations were conducted because space use data are only collected three times per year (April, August, and October). Therefore, to incorporate data from the April directly preceding the birth of the lamb, whilst having enough data to estimate home ranges, we used spatial data from the four census periods (April–April) preceding the observations. Second, the resources available to a female prior to lactation are likely to influence her body weight or condition and therefore may also affect her provisioning over the maternal care period (Landete-Castillejos et al. 2003). We used annual home range quality and resource selection functions to provide a more complete picture of the relationship between resource availability and maternal care by enabling us to characterize variation in access to a wider range of plant communities and making it possible to assess the impact of characterizing home range quality at a particular temporal scale. We estimated annual home ranges and home range quality metrics for each individual in the same way as the lifetime home ranges, but using only location data from the 4 census periods (April–April) preceding the time of observation. Because using the mean percentage cover of *H. lanatus* as a measure of home range quality may be sensitive to variation in home range size we calculated an alternative measure of quality for annual home ranges in order to assess the robustness of our results. We weighted the percentage cover of *H. lanatus* in each hectare covered by an individual's utilization distribution (70% isopleth) by the amount of the hectare contained within the utilization distribution before summing these values to give an estimate of the area of an individual's home range that was covered by *H. lanatus*.

We also estimated individual resource selection functions for the year before each field season in order to obtain a more thorough

measure of an individual's use of habitat. Resource selection functions (RSFs) estimate habitat selection by comparing the characteristics of locations used by organisms against those not used (Manly et al. 2002); however, because we are unable to explicitly ascribe absences to locations, our data correspond to a used/available design (Boyce et al. 2002). By using RSFs, we could characterize each individual's selection for multiple plant communities, including HA grassland. We estimated second-order habitat selection; that is, the selection of the home range (Johnson 1980), as this most closely corresponds to the home range quality measures described above. We sampled *n* used locations directly from the 95% kernel annual home range contour (calculated as above), whilst *n* available locations were sampled randomly from the area covered by the 160 hectares for which there are vegetation data (*n* was the number of census observations for each individual over the April–April preceding observation). To make use of percentage cover data for the 14 most common plant species, but reduce the number of variables included in the RSF, we used principle components analysis to derive three variables (the first 3 principal components [PC1, PC2, and PC3] which accounted for 59.3% of the variation across hectares). PC1 loaded negatively on species present in *HA* grassland (including *H. lanatus*, *Agrostis capillaris* and *Festuca rubra*) and in the maritime *Festuca-Plantago* swards (including *Plantago lanceolata* and *P. maritima*) and positively on species associated with heathland, including *Calluna vulgaris* and *Nardus stricta* (see Supplementary Figure S2). In contrast, PC2 loaded positively on species associated with HA grassland and negatively on species associated with *Festuca-Plantago* swards, whilst PC3 loaded positively on *Calluna vulgaris* (see Supplementary Figure S3). We calculated an RSF for each female using the 3 principal components as predictors in a logistic regression (Manly et al. 2002). We then extracted the coefficients from these regressions for use in subsequent models aimed at understanding how variation in resource selection was associated with variation in maternal care behaviours (see below).

Behavioural observations

We successfully tracked 34 females in 2014 and 35 females in 2015 (females were never observed in both years), all of which gave birth to singleton lambs. We focused on singletons because low twinning rates in both years (2014—18%, 2015—12%) meant that it was unlikely that we would be able to follow enough twins to enable us to detect any difference in the response of females to resource variation as a result of differences in litter size. The females varied substantially in the quality of their home ranges, with the mean percentage cover of *H. lanatus* in lifetime home ranges ranging from 9.6% to 61.5%. To monitor the behaviour of females and their lambs from birth until weaning, we made 3 trips to St. Kilda each year. The first started in mid-April and lasted until late May (2014—15/04 to 28/05, 2015—13/04 to 21/05), the second trip occurred in June (2014—23/06 to 02/07, 2015—23/06 to 05/07) and the final trip commenced in late July (2014—22/07 to 04/08, 2015—22/07 to 03/08). Focal observations were conducted once for each week of the lamb's life where possible (see Supplementary Figure S1 for an illustration of observation spread for each individual) using "Animal Behaviour Pro" (Newton-Fisher 2012). One female (BR501) and her lamb died shortly after the second observation was conducted; however, the inclusion of data for this pair did not modify the results and, therefore, we present results with these data included. Individuals were located using 10x42 binoculars (Vortex, USA) and spotting scopes (16-48x; Opticron, UK), and were then observed from a distance of at least ten meters. It was not possible for observations to be done totally blind because animals were specifically selected based on their home range quality and because there are visible differences in the vegetation across the study area; however, assistants had limited information regarding the home range quality of different animals and the quality of different communities within Village Bay. Observations were conducted between 08:00 and 19:00, and the focal watches for each individual were distributed across the day and between observers (two per trip) to prevent any between-individual differences caused by the data collection procedure. Focal observations lasted 1 hour, with lamb behaviour recorded continuously and female behaviour recorded instantaneously at 2-minute intervals (see Table 1 for descriptions of the recorded behaviours). Whenever females and lambs separated, we preferentially kept the lamb in sight in order to accurately record non-sucking behaviours. Hirta is littered with dry-stone structures known as cleits, which were used for storage by the St. Kildans, but are now used for shelter by the sheep. Sheep are very difficult to observe when inside a cleit, and we therefore ended observations when both the female and her lamb entered a cleit. We continued with observations when either the female or her lamb were inside a cleit, recording them as "Out of sight", as in this case we could be sure that no suckling events were missed. There was one case where a lamb sucked from both its mother and grandmother and in this case we recorded, but later excluded, all sucks from the grandmother prior to analysis. In total, we conducted 570 h of observations, with between 2 and 13 focal watches per female-lamb pair (Supplementary Figure S1).

Statistical analyses

For each focal observation, we calculated suckling frequency (the number of suckling events per hour regardless of length), total sucking time (the total time in seconds that a lamb spent sucking per hour), and the mean suckle duration (total sucking time divided by the frequency of suckling events). One suckling event which lasted 248 s was removed as it was a clear outlier, having likely been extended due to vigilance in response to tourist disturbance. We also calculated the frequency of failed suckling events (the number of failed suckling events per hour), denoted as a suckling bout shorter than 5 s (following Hass 1990; Birgersson and Ekvall 1994; Tollefson et al. 2011), the frequency of female terminated suckling events (the number of suckling events terminated by the female per hour), and the total time (in seconds) that a lamb spent grazing, playing, and resting during each focal watch (grazing time, playing time, and resting time, respectively). In the case of the female, we calculated the number of time points (out of 30) that she spent in each of the recorded behaviours, providing information on grazing frequency, resting frequency, and moving frequency.

Data were analysed using linear and generalized linear mixed models using the packages lme4 (Bates et al. 2015) and glmmADMB (Skaug et al. 2006) in R version 3.1.3 (R Development Core Team 2008). All models included individual identity and the date on which the observation was conducted as random effects. They also included year (two level factor), maternal age (covariate), and lamb age (covariate) as fixed effects. To understand how a female's home range quality (both lifetime and annual) influenced maternal care, we compared a subset of 10 models for each trait, that contained all combinations of the following fixed effects: a quadratic term for lamb age to determine if a nonlinear relationship was a better fit to the data, the mean percentage cover or absolute cover of *Holcus lanatus* to test for an effect of home range quality, a quadratic term for the mean percentage cover

Table 1
Descriptions of the female and lamb behaviours recorded during focal observations

Individual	Behaviour	Description
Lamb	Sucking	Recorded each time the lamb was in contact with the teat. The head is usually tilted upwards slightly and sucking is often accompanied by tail wagging and intense butting of the teat. Failed suckling events were classed as periods of suckling behaviour that lasted less than 5 s. For each suckling event, termination by either the female or lamb was noted. Female termination was characterized by the female walking off or kicking the lamb, whereas lamb termination was noted when the lamb stopped sucking of its own accord.
Lamb	Grazing	Short periods of head down movement, but where lambs were explicitly seen taking bites of grass (in the first few days of life they show interest in grass but are yet to take it into their mouth).
Lamb	Resting	When the lamb is lying down.
Lamb	Playing	Either lone play or play involving other lambs, generally characterized by short bursts of running, leaping, and head butting.
Lamb	Other	A category for all behaviours that do not fit into the other described categories. It generally consists of movement behaviour.
Lamb	Out of sight	This category was used to note periods when the lamb was not in view, whether this was because the lamb was obscured by an object, had gone out of sight during play, or had been disturbed in some way.
Female	Suckle	Noted when the female's behaviour was recorded during a suckling bout.
Female	Grazing	Head down, taking bites and short periods of head down movement between bites.
Female	Resting	Female lying down and ruminating or showing no observable activity.
Female	Moving	If the female was showing any movement not associated with grazing.
Female	Other	Periods of activity that do not fit in the other described categories. Largely made up of grooming and general alertness.
Female	Out of sight	Used to denote periods when the female was not in view.

or absolute cover of *Holcus lanatus* (again to test for a nonlinear relationship), and a first-order interaction between lamb age and the mean percentage cover or absolute cover of *Holcus lanatus* to examine whether the relationship between a given behaviour and home range quality varied with lamb age. Both lamb age and the mean percentage cover or absolute cover of *Holcus lanatus* were mean centred and scaled to reduce collinearity between power terms. These models were compared using Akaike's Information Criterion corrected for small sample size (AICc). The best model was taken to be that with the lowest AICc value (Burnham and Anderson 2002); however, if there was a more parsimonious model (i.e. with fewer terms) that had a comparable AICc (<2 units difference) then the simpler model was accepted as the best model (Burnham and Anderson 2002). We present only the best model from each analysis in the results, but the outputs of full models and the AICc scores for full and best models are available in the supporting information (Supplementary Tables S1–S4).

To understand if our results were affected by density variation within the study area we re-analysed the behavioural data using annual home range quality measures as above and the number of females with overlapping home ranges as an additional fixed effect. We used Bhattacharyya's affinity (BA) in adehabitatHR (Calenge 2006) to calculate the home range overlap/similarity for every pair of females that were alive and had more than 5 census observations in the year preceding each observation period. We then used this information to calculate the number of individuals whose utilization distribution had a BA exceeding 0.01 (BA scales from 0–1) with the utilization distribution of each behavioural female, at which point they were classed as having overlapping home ranges. For each trait we compared a set of 20 models that contained all possible combinations of the lamb age (linear and quadratic), home range quality (linear, quadratic, and first-order interaction with lamb age), and density terms. The best model was determined using AICc, as above. The results from these analyses were not qualitatively different to those from analyses excluding density and therefore they are presented in the supporting information (Supplementary Table S2).

We used a similar approach when conducting analyses to understand whether maternal care behaviour varied with habitat selection; however, in the place of the percentage cover of *H. lanatus*, we included PC1, PC2 and PC3. We therefore compared a subset of 54 models for each trait, that contained all combinations of the resource selection variables (PC1, PC2, and PC3), a quadratic term for lamb age, and a first-order interaction between each of the resource selection variables and lamb age. As for the analyses using home range quality metrics, AICc was used to compare these models, with the best model taken to be that with the lowest AICc value unless there was a more parsimonious model with a similar AICc (<2 units difference) (Burnham and Anderson 2002). Because the estimates of resource selection functions are themselves associated with error, we wanted to understand whether this impacted the results of models performed using only the parameter estimates from the logistic regression used to estimate RSFs. To do this we used the parameter estimates and standard errors from the regressions for each individual to obtain a distribution from which we selected 100 random values. We then ran our mixed models using each of these set of values, deriving a best model from each (as above) to understand how many of these models—if any—featured any of the resource selection components.

Total sucking time (with and without failed suckling events), mean suckle duration (with and without failed suckling events), and grazing time were log transformed prior to analysis in order to ensure that the distribution of the residuals had a closer approximation to normality. These behaviours, along with resting time, were then analysed using linear mixed models assuming a Gaussian distribution. We assumed a Poisson distribution when analysing suckling frequency (excluding failed suckling events), but used negative binomial mixed models (performed in glmmADMB) for suckling frequency (including failed suckling events), female grazing frequency, female resting frequency, and female moving frequency due to the overdispersion apparent in the residuals when assuming a Poisson distribution. We assumed a binomial distribution when analysing the proportion of successful suckling events, using the "bobyqa" optimizer to aid convergence. We do not present results

for playing time and the proportion of female terminated suckling events because severe zero-inflation resulted in poor residual distributions despite all transformations and error distributions employed.

To supplement the above analyses and aid in the interpretation of our behavioural results, we also investigated the effect of a female's annual home range quality on the growth of her lambs and her body condition at the end of the summer. Because only 39 lambs observed during 2014 and 2015 were caught in August catches (equating approximately to weaning), and the majority of these lambs were born to females with high quality home ranges (only seven lambs born to females with *H. lanatus* covers lower than 30%), we used data spanning the period 1985–2015 for this analysis. Similarly, we used data spanning the period 1988–2015 to maximize the sample size for body condition analyses. In order to be consistent with the behavioural work we restricted our analyses to females aged between 3 and 8 years old, which had given birth to singleton lambs. This left us with 1079 lambs (born to 533 females) for growth analyses and 1168 females for the body condition analyses. We calculated lamb growth as the change in weight (in grams) between birth in April/May and the catch in August divided by the number of days between birth and August weight measurements, and maternal body condition as the residuals from a linear regression of August body mass against hind leg length. There has been substantial debate over the accuracy of this measure of body condition (Green 2001; Schulte-Hostedde et al. 2005); however, due to data limitations we are unable to use more direct measures of condition. Both lamb growth and body condition were analysed using linear mixed effects models using lme4 (Bates et al. 2015). In both cases, maternal identity was included as a random effect, with lamb year of birth included as a random effect in growth models, whilst the year of measurement was included as a random effect in models of maternal body condition. In lamb growth models, we included the lamb's sex, maternal age, and julian birth date as fixed effects, whereas in maternal body condition models we included only the female's age as a fixed effect. To test for an association between home range quality and both lamb growth and female body condition, we then compared these models with a model that also contained the percentage cover of *H. lanatus* in a female's annual home range as a fixed effect and another model containing a quadratic term for the mean annual home range percentage cover of *H. lanatus*. In both cases, we used home ranges calculated for the year preceding the lamb's birth. These models were also compared using AICc, with the best model taken to be that with the lowest AICc unless there was a more parsimonious model with a comparable AICc.

RESULTS

Variation in home range quality

There was substantial between-individual variation in home range quality and habitat selection. Mean percentage covers of *H. lanatus* in female lifetime home ranges varied from 9.6% to 61.5%, with a similar pattern evident for annual home ranges, which had mean *H. lanatus* covers ranging from 10.2% to 64.3%. In the case of resource selection functions, there was considerable variation in the selection for the three broad community types (represented by the three principal components). The greatest variation was apparent in PC1 with beta coefficients for this principal component ranging from −12.8 to 1.0. In this case, the more negative the value, the greater the selection for plant species associated with grassland rather than species associated with heathland. The ranges for PC2 and PC3 were smaller than for PC1 but similar to each other at −0.1 to 9.6 and −0.8 to 9.9, respectively. In the case of PC2, more positive values corresponded to greater selection for species associated with HA grassland relative to *Festuca-Plantago* swards, whilst for PC3, more positive values were associated with greater selection for areas rich in *Calluna vulgaris*.

Lamb behaviours

Likelihood ratio tests of models with and without the individual identity random effect indicated that there was between individual variation in suckling frequency [with (χ^2 (1) = 5.34, P = 0.02) and without failed suckling events (χ^2 (1) = 67.65, P = < 0.0001)], mean suckle duration (without failed suckling events— χ^2 (1) = 14.07, P = 0.0002), suckling success (χ^2 (1) = 6.00, P = 0.01), and grazing time (χ^2 (1) = 5.45, P = 0.02) even when fixed effects were accounted for. As expected, lamb age was a key predictor in models for all the lamb behaviours recorded over the period of maternal care, being present in the best fit model in all cases (Table 2). This suggests that our methods were effective in capturing variation in lamb behaviours over this period. All of the measures of sucking behaviour, as well as the total time a lamb spent resting, decreased as the lamb approached weaning (Table 2). However, these relationships were non-linear, with the reduction being most pronounced within the first weeks of life (Figure 1). In contrast, the total time a lamb spent grazing during each observation increased as they approached weaning, though after around 70 days of age the total time a lamb spent grazing decreased slightly (Table 2).

We first used lifetime home range quality metrics in our analyses as the females in our study were selected based on this measure. We found no evidence for a significant association between any of the measures of sucking behaviour and the lifetime mean percentage cover of *H. lanatus* in a female's home range. Home range quality did not feature in the best fit model for any of the measures of lamb sucking behaviour (Table 2), and this result was consistent whether failed suckling events were excluded or not (Supplementary Table S3). We also found no evidence for a significant relationship between a female's home range quality and any of the non-suckling behaviours recorded, with home range quality absent from the best fit models for both grazing time and resting time (Table 2).

When we used the annual home range quality metrics we also found that the mean percentage cover of *H. lanatus* was not important in explaining any of the lamb behaviours studied (Table 2). As for the analyses using lifetime home range quality metrics, the mean percentage cover of *H. lanatus* in a female's annual home range did not feature in the best fit models for suckling frequency, mean suckle duration, suckling success, total sucking time, total grazing time, or total resting time (Table 2). Furthermore, the results for the suckling behaviours were consistent whether failed suckling events were included or not (Supplementary Table S3). We also found that our results were equivalent when the absolute cover of *H. lanatus* in a female's home range was used, with this term absent from the best fit models for all lamb behaviours (Supplementary Table S2).

Analyses using resource selection function coefficients tended to produce similar results to analyses performed using home range quality metrics, with none of the three coefficients (PC1, PC2, or PC3) featuring in best fit models for suckling frequency, mean suckle duration, total grazing time or total resting time (Table 2). These results were also consistent when failed suckling events were excluded (Supplementary Table S3). In addition, when we performed

Table 2

Parameter estimates (± standard error) from the best fit models for all lamb behaviours (with failed suckling events), using lifetime home range quality estimates, annual home range quality estimates (A corresponds to the annual mean percentage cover of *H. lanatus*, whilst B corresponds to the annual absolute cover of *H. lanatus*) and annual resource selection function coefficients

		Lifetime home range		Annual home range A		Annual home range B		Resource selection function	
Trait	Term	Est(SE)	*t*/*z**	Est(SE)	*t*/*z**	Est(SE)	*t*/*z**	Est(SE)	*t*/*z**
Suckling frequency	Lamb age (days)	−1.09(0.06)	−19.76	−1.09(0.06)	−19.76	−1.09(0.06)	−19.76	−1.01(0.06)	−17.06
	Year (2015)	0.34(0.10)	3.56	0.34(0.10)	$3.7 \times e^{-4}$	0.34(0.10)	3.56	0.31(0.11)	2.83
	Maternal age	−0.04(0.03)	−1.25	−0.04(0.03)	−1.25	−0.04(0.03)	−1.25	−0.04(0.03)	−1.26
	Lamb age^2	0.35(0.06)	5.36	0.35(0.06)	5.36	0.35(0.06)	5.36	0.34(0.07)	5.20
Mean suckle duration	Lamb age (days)	−0.35(0.05)	−7.16	−0.35(0.05)	−7.16	−0.35(0.05)	−7.16	−0.35(0.05)	−7.16
	Year (2015)	−0.03(0.08)	−0.35	−0.03(0.08)	−0.35	−0.03(0.08)	−0.35	−0.03(0.08)	−0.35
	Maternal age	0.03(0.02)	1.11	0.03(0.02)	1.11	0.03(0.02)	1.11	0.03(0.02)	1.11
	Lamb age^2	0.26(0.06)	4.54	0.26(0.06)	4.54	0.26(0.06)	4.54	0.26(0.06)	4.54
Sucking time	Lamb age (days)	−1.41(0.08)	−17.75	−1.41(0.08)	−17.75	−1.41(0.08)	−17.75	−1.43(0.08)	−17.55
	Year (2015)	0.36(0.13)	2.76	0.36(0.13)	2.76	0.36(0.13)	2.76	0.38(0.13)	2.86
	Maternal age	$-6.6 \times e^{-4}$(0.04)	−0.02	$-6.6 \times e^{-4}$(0.04)	−0.02	$6.6 \times e^{-4}$(0.04)	−0.02	0.003(0.04)	0.07
	Lamb age^2	0.49(0.09)	5.74	0.49(0.09)	5.74	0.49(0.09)	5.74	0.51(0.09)	5.81
Suckling success	Lamb age (days)	−0.10(0.11)	−0.96	−0.10(0.11)	−0.96	−0.10(0.11)	−0.96	−0.005(0.12)	−0.04
	Year (2015)	−0.17(0.17)	−1.04	−0.17(0.17)	−1.04	−0.17(0.17)	−1.04	−0.11(0.17)	−0.67
	Maternal age	0.08(0.04)	1.74	0.08(0.04)	1.74	0.08(0.04)	1.74	0.09(0.05)	1.93
	Lamb age^2	0.39(0.13)	2.98	0.39(0.13)	2.98	0.39(0.13)	2.98	0.49(0.13)	3.63
	PC1	—	—	—	—	—	—	0.002(0.06)	0.04
	PC3	—	—	—	—	—	—	−0.06(0.10)	−0.61
	Lamb age:PC1	—	—	—	—	—	—	0.24(0.06)	3.79
	Lamb age:PC3	—	—	—	—	—	—	0.26(0.09)	2.80
Grazing time	Lamb age (days)	2.86(0.13)	21.84	2.86(0.12)	21.84	2.86(0.13)	21.84	2.86(0.13)	21.84
	Year (2015)	−0.04(0.23)	−0.19	−0.04(0.23)	−0.19	−0.04(0.23)	−0.19	−0.04(0.223)	−0.19
	Maternal age	−0.004(0.07)	−0.06	−0.004(0.07)	−0.06	−0.004(0.07)	−0.06	−0.004(0.07)	−0.06
	Lamb age^2	−1.66(0.14)	−11.79	−1.66(0.14)	−11.79	−1.66(0.14)	−11.79	−1.66(0.14)	−11.79
Resting time	Lamb age (days)	−332.29(57.97)	−5.73	−332.29(57.97)	−5.73	−332.29(57.97)	−5.73	−332.29(57.97)	−5.73
	Year (2015)	−80.95(88.02)	−0.92	−80.95(88.02)	−0.92	−80.95(88.02)	−0.92	−80.95(88.02)	−0.92
	Maternal age	12.10(27.61)	0.44	12.10(27.61)	0.44	12.10(27.61)	0.44	12.10(27.61)	0.44
	Lamb age^2	150.88(62.51)	2.41	150.88(62.51)	2.41	150.88(62.51)	2.41	150.88(62.51)	2.41

**t* values are reported for linear mixed effects models whilst *z* values are reported for generalised linear mixed effects models.

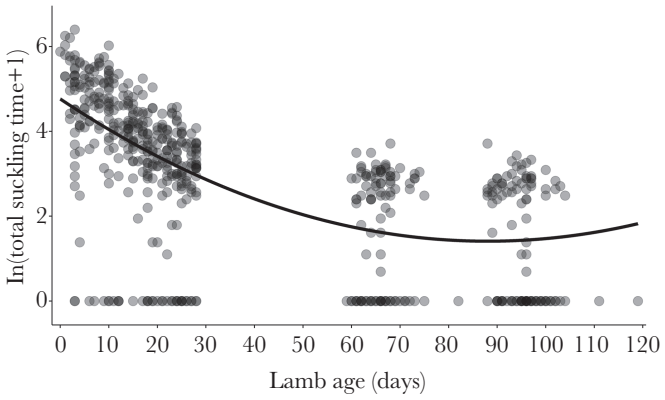

Figure 1

Total sucking time (log transformed) plotted against lamb age in days. The regression line comes from the full linear mixed model; however, to aid interpretation we plot the relationship for 2015 only.

models using resource selection coefficients that incorporated the error around the RSF parameter estimates our results were similar, with only 12 out of the 100 best fit models including any of the RSF coefficients. The one difference between the results of home range quality and RSF analyses came from models of suckling success. Suckling success was not explained by home range quality, whether lifetime or annual (Table 2). In contrast, when resource selection coefficients were used, both PC1 and PC3 featured in the best fit model for the proportion of successful suckling events in first-order interactions with lamb age. These terms indicated that the relationship between suckling success and a female's habitat selection changed as the lambs aged (Table 2). When the lambs were young, there was little difference in suckling success with a female's selection for HA grassland; however, as the lambs approached weaning, individuals born to females exhibiting greater selection for heathland (communities dominated by *C. vulgaris*, *N. stricta* etc) had greater suckling success (Fig. 2). Similarly, as lambs aged, individuals born to females that selected for plant communities rich in *Calluna vulgaris* had greater suckling success (Table 2).

Female behaviours

We also found that female behaviours varied with lamb age, with grazing frequency declining with lamb age and both resting frequency and moving frequency increasing with lamb age (Table 3). As for lamb behaviours, there was no evidence for consistent variation in female behaviour with home range quality. The mean percentage cover of *H. lanatus* in a female's lifetime home range did not feature in the best fit model for grazing frequency, moving frequency or resting frequency (Table 3). The same was generally true when we used annual home range quality metrics. Both the annual mean percentage cover of *H. lanatus* and annual absolute cover of *H. lanatus* were absent from the best fit models for all the female behaviours studied, except in the case of movement frequency when the number of overlapping females was included

(Table 3 and Supplementary Table S2). When the density term was included the absolute cover of *H. lanatus* featured in the best fit model, suggesting that females with higher quality home ranges spent more time moving per hour of observation (Supplementary Table S2). Our results were also largely comparable when we used coefficients from individual resource selection functions in place of home range quality metrics, with none of the three principal components featuring in the best fit models for grazing frequency or resting frequency (Table 3). The results for moving frequency did differ slightly when using the resource selection coefficients, with PC2 featuring in the best fit model in a first order interaction with lamb age (Table 3). This term indicated that females who selected more highly for *Festuca-Plantago* swards spent more time moving.

Lamb growth and maternal body condition

Lamb growth between birth and August varied with both birth date and sex, with late born lambs and male lambs growing more quickly over this period (Table 4). However, there was no indication that lamb growth varied in relation to the quality of their mother's home range in the year preceding their birth as this term was not included in the best fit model (Table 4). There was also no indication that the quality of a female's home range in the year preceding the birth of her lamb affected her body condition in the following August (Supplementary Figure S4). The AICc of the model including home range quality (both linear and quadratic term) was equivalent (<2 unit difference) to the best model (selected following rules of parsimony); however, it was apparent from this model that the relationship between home range quality and female body condition was very weak (Supplementary Figure S4).

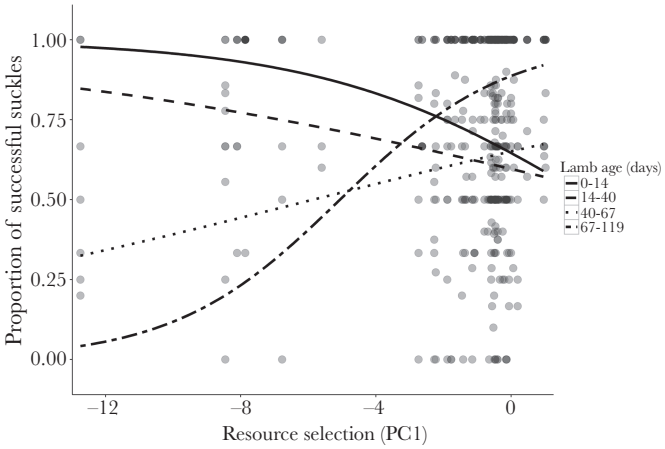

Figure 2
Plot illustrating the interaction between lamb age and PC1 in the best fit model for suckling success. The relationship between the proportion of successful suckling events in each observation (*y* axis) and individual PC1 coefficients (broadly describing the degree of selection for Festuca-Plantago swards) from resource selection functions varies depending on the age of the lamb, becoming more positive as the lamb ages. Each line represents the model prediction (from the full model) for a different set of lamb ages.

DISCUSSION

In this study, we examine the role of individual-level, as opposed to population-level, variation in resource availability on post-natal maternal care in a wild-living mammal. We found no evidence that variation in female or lamb behaviour over the period of maternal care was associated with variation in the quality of the home range occupied by a female Soay sheep. There was no indication that suckling frequency, or the mean duration of suckles varied with home range quality, and consequently there was no significant relationship between the quality of a female's home range and the total time her lamb spent sucking. There was also no indication that the quality of a female's home range influenced her lamb's grazing and resting behaviour. Similarly, we found no association between either lifetime or annual home range quality and female grazing, resting or movement frequency. Our behavioural results were supported by our analyses of lamb growth, where we found that the quality of a female's home range had no influence on the weight gain of her lambs between birth and weaning. This also suggests that lambs born to females with home ranges of differing qualities did not receive differing levels of investment. In addition to providing comparable levels of care, females were in similar condition in the August following the birth of their lamb despite having home ranges of differing qualities. This may explain why a previous analysis found no apparent relationship between home range quality and female lifespan (Regan et al. 2016).

Though it is somewhat surprising that Soay sheep females do not adjust their investment into maternal care given the quality of their home range, we feel our results are robust for the following reasons. First, our sample size of 69 individuals is large relative to

Table 3
Parameter estimates (± standard error) from best models for all female behaviours, using lifetime home range quality estimates, annual home range quality estimates (A corresponds to the annual mean percentage cover of *H. lanatus*, whilst B corresponds to the annual absolute cover of *H. lanatus*) and annual resource selection function coefficients

		Lifetime home range		Annual home range A		Annual home range B		Resource selection function	
Trait	Term	Est(SE)	*z*	Est(SE)	*z*	Est(SE)	*z*	Est(SE)	*z*
Grazing frequency	Lamb age (days)	−0.14(0.02)	−7.96	−0.14(0.02)	−7.96	−0.14(0.02)	−7.96	−0.14(0.02)	−7.96
	Year (2015)	0.06(0.03)	1.74	0.06(0.03)	1.74	0.06(0.03)	1.74	0.06(0.03)	1.74
	Maternal age	0.005(0.01)	0.48	0.005(0.01)	0.48	0.005(0.01)	0.48	0.005(0.01)	0.48
Resting frequency	Lamb age (days)	0.48(0.08)	5.79	0.48(0.08)	5.79	0.48(0.08)	5.79	0.48(0.08)	5.79
	Year (2015)	−0.43(0.17)	−2.57	−0.43(0.17)	−2.57	−0.43(0.17)	−2.57	−0.43(0.17)	−2.57
	Maternal age	−0.009(0.05)	−0.17	−0.009(0.05)	−0.17	−0.009(0.05)	−0.17	−0.009(0.05)	−0.17
Moving frequency	Lamb age (days)	0.11(0.06)	1.73	0.11(0.06)	1.73	0.11(0.06)	1.73	0.20(0.09)	2.34
	Year (2015)	0.43(0.17)	2.48	0.43(0.17)	2.48	0.43(0.17)	2.48	0.47(0.17)	2.68
	Maternal age	−0.02(0.05)	−0.47	−0.02(0.05)	−0.47	−0.02(0.05)	−0.47	−0.04(0.05)	−0.84
	PC2	—	—	—	—	—	—	−0.10(0.06)	−1.65
	Lamb age:PC2	—	—	—	—	—	—	0.08(0.05)	−1.59

Table 4

Parameter estimates (± standard error) for full and best models of lamb growth (between birth and weaning) and maternal body condition

		Full model		Best model	
	Term	Est(SE)	*t*	Est(SE)	*t*
Lamb growth	Maternal age	0.13(0.26)	0.48	0.12(0.26)	0.48
	Sex (male)	14.43(0.80)	18.02	14.43(0.80)	18.02
	Birth date	0.57(0.09)	6.41	0.57(0.09)	6.50
	HR quality	−0.06(0.22)	−0.26	—	—
	HR quality^2	$7.8 \times e^{-4}$(0.003)	0.27	—	—
Maternal body condition	Maternal age	0.20(0.03)	7.36	0.20(0.03)	7.32
	HR quality	−0.03(0.07)	−0.41	—	—
	HR quality^2	−0.10(0.06)	−1.62	—	—

In both cases home range qualities were derived from annual home ranges.

that of many similar studies using wild populations (e.g. Tremblay et al. 2004—26 individuals, Robertson et al. 1992—44 females with singletons, and Andersen et al. 2000—24 individuals). Second, by observing each female and her lamb over the entire period of maternal care, our results were not biased by examining the relationship between resource availability and care over a shorter time scale. Third, we recorded non-suckling behaviours both of the female and the lamb, making it possible to examine whether the female or lamb adjusted such behaviours in response to the pattern of care. Finally, although the characterization of the resources available to an individual is complex, our results were robust across different measure of resource use, suggesting that resource variation was accurately captured. When using coefficients from RSFs, we found an association between female movement frequency and resource use that was not apparent in analyses using *H. lanatus* cover. This result suggests that females who select for *Festuca-Plantago* dominated swards moved more frequently during observations. It is not particularly surprising that we did not detect this trend with models using only *H. lanatus* covers as the amount of HA grassland in a female's home range is unlikely to correlate strongly with the amount of *Festuca-Plantago* sward within their home range, particularly as *Festuca-Plantago* swards are relatively restricted to the west of the study area. Individuals in these areas are also the least accustomed to human activity and as a result, are the most sensitive to human disturbance. It is therefore possible that this result is due to increased movements made by these individuals as a result of tourist disturbance.

Variation in resource availability is expected to alter the amount of parental care through its effects on the relative costs and benefits of parental care (Clutton-Brock 1991). Despite this, it has often proved difficult to demonstrate a link between resource availability and parental care behaviour, as illustrated by our work and numerous other studies (e.g. Whittingham and Robertson 1994, Andrews et al. 2017). It seems unlikely that variation in resource availability would not affect the costs and benefits of parental care, but it is possible that this effect does not translate into the predicted difference in parental care behaviour. In our case we can exclude any effects due to the behaviour of a partner as only females provide care in this species. It is possible that behavioural measures of parental care may not accurately reflect the transfer of resources from parent to offspring. For instance, in the case of mammals, there is criticism surrounding the use of suckling behaviour as an indicator of milk intake (summarised in Cameron (1998) and maternal investment during lactation. For example, mothers may vary in the nutritional content of their milk, and offspring may therefore receive very different amounts of nutrition for the same amount of time spent sucking (Skibiel and Hood 2015). Furthermore, individual offspring may differ in the efficiency with which they obtain milk (Cameron 1998). Despite these concerns, we believe that our approach has characterized variation in parental care in Soay sheep. First, by observing individuals at various times throughout the day and across the entire maternal care period, it is unlikely that our results are biased due to within-day or seasonal variation in suckling behaviour. Second, by measuring non-suckling behaviours of both a female and her lamb, we obtained a more complete picture of each individual's decisions over this period. For example, by recording grazing behaviour we were able to look for evidence of compensation by the female or her lamb for the level of parental care. Finally, because of the long-term nature of the St. Kilda Soay sheep project, we had access to a larger sample of growth data to validate any results from our behavioural observations. The results of this analysis confirm that variation in home range quality does not influence post-natal maternal care. This period includes a significant portion of time over which the lamb is able to supplement the nutrition gained from its mother by grazing, which may complicate any analysis of the relationship between home range quality and maternal care. Nevertheless, our results show that lamb grazing behaviour does not vary with home range quality, supporting our suggestion that females with home ranges that differ in quality invest similarly into maternal care.

Our finding that environmental conditions have no effect on parental care has implications for our understanding of reproductive strategies in ungulates. Previous studies suggest that female ungulates tend to favour their own survival and reproduction over that of their offspring under poor conditions, thereby exhibiting a conservative reproduction strategy. For example, studies on bighorn sheep (*Ovis canadensis*) and white-tailed deer (*Odocoileus virginianus*) suggest that females exhibit bet-hedging strategies, such that there is little change in female mass/survival but there are significant reductions in offspring mass/survival when conditions are poor (Festa-Bianchet and Jorgenson 1998; Therrien et al. 2007; Martin and Festa-Bianchet 2010). In addition, other studies show that variation in forage quality between years or between populations is associated with behavioural differences or variation in offspring growth. For example, mountain goat (*Oreamnos americanus*) kids in Alberta, Canada, grow faster in years where forage quality is high (Côté and Festa-Bianchet 2001). Similarly, a recent study on Appennine chamois (*Rupicapra pyrenaica ornata*) found reductions in maternal care when pasture quality was poor (Scornavacca et al. 2016). Long-lived iteroparous species such as ungulates are

expected to follow a conservative reproduction strategy, given that parents should favour their own reproduction when resource scarcity has a smaller impact on the future reproduction of the parent compared to that of the offspring (Clutton-Brock 1991). For this reason, we would also expect female Soay sheep to show such a pattern because their fitness is determined to a greater degree by their own survival and reproduction than that of offspring from any single litter (Clutton-Brock et al. 1996). However, in contrast to the above studies, we found no evidence that reduced home range quality altered the level of maternal care or the mass gain of lambs. Therefore, there was little evidence to suggest that female Soay sheep exhibit a conservative reproductive strategy in response to spatial variation in resource availability.

One of the key reasons for why we did not find evidence for a conservative reproductive strategy in this study may lie in the specific biology of the St. Kilda Soay sheep. This population is characterized by instability, with periodic population crashes in which up to 70% of the animals on the island die (Clutton-Brock et al. 2004). Previous research suggests that Soay sheep females do not base decisions about reproductive investment upon information about future trends in population density, instead using information on current nutrition, body mass, and age (Marrow et al. 1996). Potentially, all females in our study were able to meet the costs of lactation regardless of the area in which their home range was located. Given that they were likely to be of high quality as heavier females are more likely to survive winter (Clutton-Brock et al. 1996), and that competition for vegetation during the summer is low due to the high productivity during this period (Crawley et al. 2004), all of our study females may have been able to counteract the costs of providing a high level of maternal care by consuming high quality resources during the high productivity period. Indeed, some studies using other systems have suggested that increased nutrient intake may be a cause for the absence of costs of reproduction (e.g. Hamel et al. 2009). The ability of the females to compensate for the costs experienced due to providing maternal care might explain why we did not detect any variation in lamb weight gain between birth and August given variation in female home range quality/resource selection, and why a previous study found no indication that lamb survival to weaning varied with the mean percentage cover of *H. lanatus* in a female's lifetime home range (Regan et al. 2016). Similarly, it may explain why lambs born to mothers with home ranges of higher quality have greater suckling success early in the season when vegetation is still limiting, whilst the opposite is true later in the summer when resource availability is high. This may indicate that females that differ in their use of space exhibit slightly different patterns of care over this period despite provisioning similarly over the total maternal care period. However, this result was driven partially by a lack of data for individuals with very negative PC1 and positive PC3 coefficients. Therefore to validate this interpretation, it would be necessary to study females that were more evenly distributed across the continuum of PC1 and PC3 values.

In both 2014 and 2015, twinning rates were low and we were therefore unable to include any twin litters in our sample. The reproductive costs of having twins is likely to be greater than the costs resulting from having a singleton. As a result, the benefit of having a high quality home range may be more pronounced for females with twins. This is particularly pertinent given that, in many of the ungulate populations where conservative reproductive strategies have been illustrated, twinning does not occur or is very rare [e.g. mountain goat (Côté and Festa-Bianchet 2001), bighorn sheep (Gaillard et al. 2000), chamois (Serrano et al. 2015)]. These studies may have been better capturing the behaviour of individuals experiencing the greatest costs as a result of providing care. However, we feel that the lack of twins in our study is unlikely to be responsible for our results given that only the heaviest females give birth to twins (Clutton-Brock et al. 2004) and these individuals are likely to be able to better cope with the costs of providing care. Such a relationship may mean that an association between habitat use and maternal care provisioning would still be absent even if twin litters were included. Given the marked fluctuations in population density on St. Kilda, the conditions in the year when observations are conducted are likely to be important in determining the behavioural patterns observed. Indeed, the study by Robertson et al. (1992) showed that suckling behaviour varies between years in St. Kilda Soay sheep. If we had conducted our observations in years where density in the previous winter had been low, the majority of individuals would have been in good condition in Spring, such that there would be little variation in the care they provide. This was not however the case, with high population density in the summer preceding both years of observation, at 545 individuals in the study area in the August of 2013 and 482 in the August of 2014. This is in contrast to recent lows of 362 and 335 in 2012 and 2002. We must consider the fact that variation in local density across the study area might have precluded an association between maternal care and home range quality, as higher density in areas of high quality might result in these areas being devalued. However, sheep consistently favour *Holcus-Agrostis* grassland, even when densities are high, potentially as a result of this community being more resilient to grazing pressure than other community types including wet and dry heath (Jones et al. 2005). Therefore, our result is unlikely to be entirely driven by variation in local density.

Our work adds to the existing literature on the effects of resource availability on parental care by examining the effect of spatial variation in resource availability quantified at the individual scale. In contrast, many of the previous studies have used resource availability estimates at the study area scale to study the effect of temporal variation in resources (e.g. Rachlow and Bowyer 1994 and Andersen et al. 2000), or have examined the effect of spatial variation in resource availability by estimating resource quantity/quality at scales above that of the individual home range (e.g. regions differing in the availability of nutritious pasture [Scornavacca et al. 2016]). Individuals are more likely to respond to the resource availability they experience in their home range than to the resources available in the study area or the area in which the population persists because it is the resource availability at this scale that will determine the costs and benefits of care. Furthermore, different parts of a study area may vary in how the quantity/quality of resources varies over time, or indeed in more subtle fine-scale spatial patterns in resource availability. It is also likely that an individual's response to temporal variation in the environment, for example variation in density and weather conditions between years may be conditional on the environmental conditions it experiences on a within-year basis. We therefore feel that there is a need to conduct further studies based on the approach used in our study, which quantify resource availability at the individual scale in order to understand how environmental conditions influence the behaviour of individuals. Movement ecology has provided the tools to quantify resource availability at the individual scale, and though the necessary data can be hard to come by we hope that the advance in tracking technologies, combined with reductions in the cost of using these technologies will make more studies of this kind possible.

In conclusion, we find that female Soay sheep vary substantially in their home range quality and in their selection for different plant communities, but there is nevertheless no evidence that home range quality influences their investment into maternal care, as indicated by both suckling behaviour and estimates of lamb growth over the summer. There was no evidence that either the female or her lamb adjusted any of the non-suckling behaviours measured (such as grazing or resting). This suggests that females inhabiting areas of Village Bay with poorer vegetation did not compensate for the level of care they provided by for example spending a greater amount of their time grazing. Our study suggests that female Soay sheep with poorer quality home ranges do not maintain their own survival and reproduction at a cost to the survival of their lambs. We suggest that this is because females giving birth to a lamb in spring, particularly following high densities in the preceding winter, are in relatively good condition, and that resources are not limiting during the summer. This may mean that no matter where a female's home range is located, she is able to offset the costs of lactation by consuming additional resources. Our results demonstrate the need to examine the effect of resource variation quantified at the individual scale on individual reproductive investment decisions. Combining this approach with studies examining the effect of temporal variation in the environment on reproductive investment decisions may provide us with a more complete picture of the influence of resource availability on reproductive investment in natural populations.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Regan et al. (2017).

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REFERENCES

Allan E, Crawley MJ. 2011. Contrasting effects of insect and molluscan herbivores on plant diversity in a long-term field experiment. Ecol Lett. 14:1246–1253.

Andersen R, Gaillard JM, Linnell JDC, Duncan P. 2000. Factors affecting maternal care in an income breeder, the European roe deer. J Anim Ecol. 69:672–682.

Andrews CP, Kruuk LEB, Smiseth PT. 2017. Evolution of elaborate parental care: phenotypic and genetic correlations between parent and offspring traits. Behav Ecol. 28:39–48.

Bales K, French JA, Dietz JM. 2002. Explaining variation in maternal care in a cooperatively breeding mammal. Anim Behav. 63:453–461.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw. 67:1–48.

Birgersson B, Ekvall K. 1994. Suckling time and fawn growth in fallow deer (Dama dama). J Zool. 232:641–650.

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA. 2002. Evaluating resource selection functions. Ecol Model. 157:281–300.

Brouwer L, van de Pol M, Cockburn A. 2014. The role of social environment on parental care: offspring benefit more from the presence of female than male helpers. J Anim Ecol. 83:491–503.

Burnham KP, Anderson DR. 2002. Information and likelihood theory: a basis for model selection. In: Burnham K, Anderson D, editors. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York: Springer-Verlag New York. p. 49–97.

Calenge C. 2006. The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. Ecol Model. 197:516–519.

Cameron E. 1998. Is suckling behaviour a useful predictor of milk intake? A review. Anim Behav. 56:521–532.

Clutton-Brock TH. 1991. The evolution of parental care. Princeton (NJ): Princeton University Press.

Clutton-Brock TH, Pemberton JM, Coulson T, Stevenson IR, Maccoll ADC. 2004. The Sheep of St Kilda. In: Clutton-Brock TH, Pemberton JM, editors. Soay sheep: dynamics and selection in an island population. Cambridge (UK): Cambridge University Press. p. 17–51.

Clutton-Brock TH, Stevenson IR, Marrow P, MacColl AD, Houston AI, McNamara JM. 1996. Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. J Anim Ecol. 65:675.

Coltman DW, Pilkington JG, Pemberton JM. 2003. Fine-scale genetic structure in a free-living ungulate population. Mol Ecol. 12:733–742.

Côté SD, Festa-Bianchet M. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia. 127:230–238.

Coulson T, Albon S, Pilkington J, Clutton-Brock T. 1999. Small-scale spatial dynamics in a fluctuating ungulate population. J Anim Ecol. 68:658–671.

Crawley MJ, Albon SD, Bazely DR, Milner JM, Pilkington JG, Tuke AL. 2004. Vegetation and sheep population dynamics. In: Clutton-Brock TH, Pemberton JM, editors. Soay sheep: dynamics and selection in an island population. Cambridge (UK): Cambridge University Press. p. 89–111.

Dixon A, Ross D, O'Malley SLC, Burke T. 1994. Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. Nature. 371:698–700.

Festa-Bianchet M, Jorgenson JT. 1998. Selsh mothers: reproductive expenditure and resource availability in bighorn ewes. Behav Ecol. 9:144–150.

Fontaine JJ, Martin TE. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. Ecol Lett. 9:428–434.

Gaillard JM, Festa-Bianchet M, Delorme D, Jorgenson J. 2000. Body mass and individual tness in female ungulates: bigger is not always better. Proc R Soc B. 267:471–477.

Gaillard JM, Yoccoz NG. 2003. Temporal variation in survival of mammals: A case of environmental canalization? Ecology. 84:3294–3306.

Green AJ. 2001. Mass/length residuals: measures of body condition or generators of spurious results? Ecology. 82:1473–1483.

Gwynne D, Milner C, Hormung M. 1974. The vegetation and soils of Hirta. In: Jewell PA, Milner C, Boyd JM, editors. Island survivors: the ecology of the Soay sheep of St Kilda. London: Athlone Press. p. 36–87.

Hamel S, Côté SD, Gaillard JM, Festa-Bianchet M. 2009. Individual variation in reproductive costs of reproduction: high-quality females always do better. J Anim Ecol. 78:143–151.

Hass CC. 1990. Alternative Maternal-Care Patterns in Two Herds of Bighorn Sheep. J Mammal. 71:24–35.

Hasselquist D, Kempenaers B. 2002. Parental care and adaptive brood sex ratio manipulation in birds. Philos Trans R Soc B Biol Sci. 357:363–372.

Huang WS, Wang HY. 2009. Predation risks and anti-predation parental care behavior: an experimental study in a tropical skink. Ethology. 115:273–279.

Johannesson B, Johannesson K. 1996. Population differences in behaviour and morphology in the snail Littorina saxatilis: phenotypic plasticity or genetic differentiation? J Zool. 240:475–493.

Johnson DH. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology. 61:65–71.

Jones OR, Crawley MJ, Pilkington JG, Pemberton JM. 2005. Predictors of early survival in Soay sheep: cohort-, maternal- and individual-level variation. Proc R Soc Lond B Biol Sci. 272:2619–25.

Jones OR, Pilkington JG, Crawley MJ. 2006. Distribution of a naturally fluctuating ungulate population among heterogeneous plant communities: ideal and free? J Anim Ecol. 75:1387–1392.

Kie JG. 2013. A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. Anim Biotelemetry. 1:13.

Landete-Castillejos T, García A, Gómez JA, Molina A, Gallego L. 2003. Subspecies and body size allometry affect milk production and composition, and calf growth in red deer: comparison of *Cervus elaphus* hispanicus and *Cervus elaphus* scoticus. Physiol Biochem Zool. 76:594–602.

Lessells C. 2012. Sexual conflict. In: Royle NJ, Smiseth PT, Kölliker M, editors. The evolution of parental care. Oxford (UK): Oxford University Press. p. 150–170.

MacColl AD, Hatchwell BJ. 2003. Sharing of caring: nestling provisioning behaviour of long-tailed tit, Aegithalos caudatus, parents and helpers. Anim Behav. 66:955–964.

Manly B, McDonald L, Thomas DI, McDonald TI, Erickson WP. 2002. Resource selection by animals. 2nd ed. Dordrecht (The Netherlands): Kluwer Academic Publishers.

Markman S, Pinshow B, Wright J. 2002. The manipulation of food resources reveals sex-specific trade-offs between parental self-feeding and off spring care. Proc R Soc Lond B Biol Sci. 269:1931–8.

Marrow P, Mcnamara JM, Houston AI, Stevenson IR, Clutton-Brock TH. 1996. State-dependent life history evolution in Soay sheep: dynamic modelling of reproductive state-dependent life history evolution in Soay sheep: dynamic modelling of reproductive scheduling. Philos Trans Biol Sci. 351:17–32.

Martin JGA, Festa-Bianchet M. 2010. Bighorn ewes transfer the costs of reproduction to their lambs. Am Nat. 176:414–423.

Møller AP, Birkhead TR. 1993. Certainty of paternity covaries with paternal care in birds. Behav Ecol Sociobiol. 33:261–268.

Moyes K. 2007. Demographic consequences of individual variation [PhD thesis]. [Canterbury (UK)] University of Kent.

Newton-Fisher N. 2012. Animal Behaviour Pro (Version 1.0) [Mobile application software] [cited: 2013 November 29]. Available from: http://itunes.apple.com.

Öberg M, Arlt D, Pärt T, Laugen AT, Eggers S, Low M. 2015. Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. Ecol Evol. 5:345–356.

R Development Core Team. 2008. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Rachlow JL, Bowyer RT. 1994. Variability in maternal behavior by Dall's sheep: environmental tracking or adaptive strategy? J Mammal. 75:328–337.

Regan CE, Pilkington JG, Pemberton JM, Crawley MJ. 2016. Sex differences in relationships between habitat use and reproductive performance in Soay sheep (*Ovis aries*). Ecol Lett. 19:171–179.

Regan CE, Pilkington JG, Smiseth PT. 2017. Data from: female Soay sheep do not adjust their maternal care behavior to the quality of their home range. Dryad Digital Repository. http://dxdoiorg/105061/dryad6nk15.

Robertson A, Hiraiwa-Hasegawa M, Albon SD, Clutton-Brock TH. 1992. Early growth and sucking behaviour of Soay sheep in a fluctuating population. J Zool. 227:661–672.

Russell AF, Langmore NE, Gardner JL, Kilner RM. 2008. Maternal investment tactics in superb fairy-wrens. Proc R Soc Lond B Biol Sci. 275:29–36.

Schulte-Hostedde AI, Zinner B, Millar JS, Hickling GJ. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology. 86:155–163.

Scornavacca D, Lovari S, Cotza A, Bernardini S, Brunetti C, Pietrocini V, Ferretti F. 2016. Pasture quality affects juvenile survival through reduced maternal care in a mountain-dwelling ungulate. Ethology. 122:807–817.

Serrano E, Colom-Cadena A, Gilot-Fromont E, Garel M, Cabezón O, Velarde R, Fernández-Sirera L, Fernández-Aguilar X, Rosell R, Lavín S, et al. 2015. Border disease virus: an exceptional driver of chamois populations among other threats. Front Microbiol. 6:1307–1316.

Skaug H, Fournier D, Nielsen A. 2006. glmmADMB: Generalized linear mixed models using AD Model Builder [cited: 2016 April 14]. Available from: http://glmmadmb.r-forge.r-project.org/.

Skibiel AL, Hood WR. 2015. Milk matters: offspring survival in Columbian ground squirrels is affected by nutrient composition of mother's milk. Front Ecol Evol. 3:111–121.

Smiseth PT, Kölliker M, Royle NJ. 2012. What is parental care? In: Royle NJ, Smiseth PT, Kölliker M, editors. The evolution of parental care. Oxford (UK): Oxford University Press. p. 1–14.

Stahlschmidt ZR. 2011. Taxonomic chauvinism revisited: insight from Parental Care Research. PLoS One. 6:e24192.

Stopher KV, Walling CA, Morris A, Guinness FE, Clutton-Brock TH, Pemberton JM, Nussey DH. 2012. Shared spatial effects on quantitative genetic parameters: Accounting for spatial autocorrelation and home range overlap reduces estimates of heritability in wild red deer. Evolution. 66:2411–2426.

Therrien JF, Côté SD, Festa-Bianchet M, Ouellet JP. 2007. Conservative maternal care in an iteroparous mammal: a resource allocation experiment. Behav Ecol Sociobiol. 62:193–199.

Thierry AM, Massemin S, Handrich Y, Raclot T. 2013. Elevated corticosterone levels and severe weather conditions decrease parental investment of incubating Adélie penguins. Horm Behav. 63:475–483.

Tollefson TN, Shipley LA, Myers WL, Dasgupta N. 2011. Forage quality's influence on mule deer fawns. J Wildl Manage. 75:919–928.

Tremblay I, Thomas D, Blondel J, Perret P, Lambrechts MM. 2004. The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits Parus caeruleus. Ibis. 147:17–24.

Tufto J, Andersen R, Linnell J. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. J Anim Ecol. 65:715–724.

Whittingham LA, Robertson RJ. 1994. Food availability, parental care and male mating success in red-winged blackbirds (*Agelaius phoeniceus*). J Anim Ecol. 63:139–150.

Winkler DW. 1987. A general model for parental care. Am Nat. 130:526–543.

Wong JWY, Kölliker M. 2012. The effect of female condition on maternal care in the European earwig. Ethology. 118:450–459.